University of Alberta

The Impact of Small Mammals on Natural Regeneration of White Spruce after Logging.

by

Susan Heidi Peters

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ABSTRACT

Through this study, I evaluated the impact of pre- and post-dispersal seed predation by small mammals on white spruce regeneration after logging in the mixedwood boreal forest of Alberta, Canada. I quantified the proportion of cones harvested by red squirrels from white spruce seed trees retained within cutblocks and trees in the adjacent forest, in a year of moderate cone production (average 1733 cones/tree in 1998). Post-dispersal seed predation, primarily by deer mice and red-backed voles, was quantified by comparing seedling recruitment in exclosures to unprotected plots, across a range of sown seed densities representing the natural range of variation in seed production. Compared to previous years, voles were abundant, while mouse populations were low in 1998. Red squirrels harvested 43% (30 – 55%) of cones on seed trees and 56% (48 – 63%) from trees in the forest. Seed trees retained in large patches had a significantly higher proportion of cones harvested (51%) than those retained as singles (33%). Mice and voles reduced recruitment density by 66 – 90% across the seed densities tested. There was no difference in small mammal foraging at the forest edge versus within the cutblock. This study demonstrated the potential of seed predators to limit white spruce regeneration in years of moderate cone production. To minimize squirrel cone harvesting from seed trees, forest managers should avoid retaining trees as large patches within cutblocks.

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CHAPTER 1

GENERAL INTRODUCTION

Natural regeneration of a plant requires the availability of seeds and appropriate microsites for germination. These two crucial elements of regeneration must coincide in space and time. When the number of seeds available limits the regeneration of a plant, factors that influence the availability of seeds will likely affect seedling recruitment density (Crawley 1992). Seed predation is one factor that can reduce the availability of seeds for regeneration (Louda 1989). For plant species with specific seedbed requirements for germination, the abundance of germination microsites may be another important limiting factor (Andersen 1989). If microsites are limiting, the relationship between seed availability and seedling recruitment is complex.

Many plants experience heavy pre- and post-dispersal seed predation by animals (Janzen 1971). A large body of literature documents extensive seed predation in old-fields (Myster and Pickett 1993, Ostfeld *et al.* 1997, Whelan *et al.* 1990), deserts (Bowers 1988), grasslands (Hoffmann *et al.* 1995) and forests (Radvanyi 1966, Sullivan 1979). Few studies have determined whether seed predation is relevant to plant populations (but see Louda *et al.* 1990). However, for some species determining how seed predation affects the population is essential to understanding regeneration patterns after a disturbance.

Seed predation is most likely to limit the population of a plant species that depends on seeds for regeneration, has no reliable bank of seeds to draw upon after a disturbance, and has the availability of seeds reduced below that of favorable germination microsites (Crawley 1992, Andersen 1989). Factors that contribute to low seed availability, either temporally or spatially, increase the likelihood that seed predation will limit recruitment. Two important factors contributing to low seed availability are: low plant (seed source) density and low annual seed production.

Low seed availability due to the relative scarcity of seed sources in areas disturbed by logging or wildfire, may increase the impact of seed predation on regeneration. Logging in Alberta's boreal mixedwood forest has rapidly increased since the early

1990's, with possible large-scale repercussions on forest regeneration. White spruce (*Picea glauca*) is one of the dominant tree species of the mixedwood forest (Strong and Leggat 1992). Successful regeneration of white spruce is important in order to sustain the mixedwood forest, yet this is considered to be the most serious silvicultural challenge (Lieffers and Beck 1994). Forest managers have addressed the problem of seed limitation by retaining white spruce seed trees in logged areas to serve as natural seed sources. Soil scarification is done to create favorable mineral soil microsites and increase germination of white spruce seeds in logged areas (Lees 1963, Lyon and Robinson 1977, Quaite 1956). However, with increased availability of germination microsites on mineral soil, loss of seeds to predators is more likely to limit recruitment. The ability of seed predators to limit the supply of white spruce seeds and influence recruitment of seedlings in seed tree cutblocks has not been addressed.

Patterns of annual seed production in species subject to heavy seed predation often show large year to year fluctuations (Silvertown 1980). Periodic synchronous production of large seed crops (mast seeding) followed by several years of low cone production is commonly cited as an anti-predator adaptation that satiates seed predators with more seeds than they can consume in mast years and starves them during years of low cone production (Janzen 1971). This implies a functional (individual) and numerical (population) response (Holling 1959) of seed predators to seed production. Field studies of common seed predators, such as small mammals, have demonstrated a functional response to food density in which consumption increases with density up to a point and then plateaus (Vickery 1979, Price and Jenkins 1986; but see Hulme and Hunt 1999).

Predator populations that are dependent on seed crops for survival are likely to fluctuate with seed production. This has been shown in red squirrels in Alberta (Kemp and Keith 1970), in voles in deciduous forests of Europe (Pucek *et al.* 1993, Jensen 1982, Selas 1997) and eastern United States (Wolff 1996), and in mice in coniferous forest in Oregon (Gashwiler 1979). Low predator populations, resulting from low seed abundance during the intermast period, are unable to increase rapidly enough to consume the entire mast crop. Thus, a higher proportion of seeds escape consumption during mast years. Some empirical studies have shown that a higher proportion of tree seeds survive in mast

years (Jensen 1982, Crawley and Long 1995, literature review in Silvertown 1980). There is limited empirical evidence that predator satiation increases the proportion of surviving seeds of white spruce in mast years (Dale *et al.* in press, Silvertown 1980, Waldron 1965).

White spruce has a regeneration strategy that is unique to tree species in the mixedwood forest. It is a masting species with year to year fluctuations in seed production that can vary 10-fold or more (Nienstaedt and Zasada 1990). It depends entirely on annual seed production to regenerate after a disturbance (Nienstaedt and Zasada 1990), but does not have a persistent seed bank in the soil (Johnson and Fryer 1996, Rowe 1955). The cones of white spruce are non-serotinous and fall off overwinter, so seeds are not available for regeneration for more than one year (Coates *et al.* 1994). Other tree species of the mixedwood forest use different regeneration strategies. Trembling aspen (*Populus tremuloides*) reproduces asexually by suckering from underground roots, relying very little on reproduction from seed (Fowells 1965). Jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) produce serotinous or semi-serotinous cones that retain their seeds for up to 10 years, until fire opens the cones to release the seeds (Johnson 1992). The unique regeneration strategy of white spruce makes the fate of seeds, before and after dispersal, critical to its ability to colonize and regenerate within a disturbance.

Red squirrels (*Tamiasciurus hudsonicus*) are the primary vertebrate cone predator of white spruce (Halvorson 1986). They are conifer specialists, relying largely on conifer seeds for overwinter survival (Rusch and Reeder 1978, Smith 1968). They cut cones from trees in late summer and early fall, after seeds are mature, but before they are dispersed. White spruce seeds are unlikely to germinate in squirrel cone caches due to the unsuitable seedbed and low seed viability after 1 year in the cache (Brink and Dean 1966, Niensteadt and Zasada 1990). Consequently, squirrels directly reduce the availability of white spruce seeds for regeneration. Cone harvesting by tree squirrels in other forest systems has ranged from greater than 80% of limber pine (*Pinus flexilis*) and white pine (*P. strobiformis*) cone crops (Benkman *et al.* 1984), 54% of sugar pine cone crop (*P. lambertiana*) (Tevis 1953), and 19-82% of ponderosa pine (*P. ponderosa*) cone crop

(Halvorson 1986). White spruce seeds may also be lost to cone insects and birds, however this was not quantified in the current study.

After seeds are dispersed in fall, they are vulnerable to predation until they germinate the following summer. The most important post-dispersal predators of white spruce are deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*) (Radvanyi 1966). In Radvanyi's study, mice and voles were responsible for 71% of the white spruce seeds that were predated. This represented 35% of the total number of seeds monitored. Deer mice and red-backed voles are the most common seed-eating small mammals in Alberta's mixedwood boreal forest (Moses and Boutin, in review). These species are often abundant in cutblocks immediately after logging (Kirkland 1990). Seeds constitute a major portion of the diet of deer mice (Whitaker 1997). Voles have a more variable diet of fungi, lichen, seeds, bark, insects and herbaceous vegetation, with the importance of seeds increasing in winter when herbaceous vegetation dies (Hansson 1985, Martell 1981, Maser *et al.* 1978, Schloyer 1977). Despite evidence of population fluctuations with seed production in Europe and eastern United States (Pucek *et al.* 1993, Jensen 1982, Selas 1997, Wolff 1996), there is currently no empirical evidence for mouse or vole fluctuations with white spruce seed production in the boreal mixedwood forest.

This research was prompted by a lack of information on the impact of seed predation on white spruce recruitment, despite the importance of natural regeneration of white spruce after logging in the mixedwood forest. The first objective was to determine the magnitude and patterns of red squirrel cone harvests from white spruce trees, in a year of moderate cone production (Chapter 2). I used cutblocks with seed trees retained in a range of densities (3 - 49 trees/ha) and spatial arrangements (single trees to large patches). This yielded information for forest managers regarding the relationship between the density and spatial arrangement of seed trees, squirrel cone harvesting patterns, and the resulting density of seed rain.

The second objective of this research was to quantify the impact of post-dispersal seed predators on white spruce seedling recruitment, across a range of initial seed densities typical of the natural range of variation in annual seed production (Chapter 3). I monitored recruitment densities in exclosures and unprotected plots with seed densities of

100 – 1000 seeds/m^2. I also assessed the seed removal rates of small mammals given different seed densities at forest edges and within the cutblocks. The functional response of small mammals to different seed densities and their impact on patterns of white spruce recruitment will be discussed.

In Chapter 4, the pre- and post-dispersal seed predation data were combined to assess their cumulative impact on seed availability and recruitment density. Implications of this research for forest management will be discussed.

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CHAPTER 2

MAGNITUDE AND PATTERNS OF CONE HARVESTING BY RED SQUIRRELS (*Tamiasciurus hudsonicus*) FROM WHITE SPRUCE IN LOGGED AREAS

INTRODUCTION

White spruce (*Picea glauca*) is one of the dominant tree species of the boreal mixedwood forest (Strong and Leggat 1992). After a disturbance, white spruce regeneration is temporally and spatially variable, depending on seed sources and seedbed conditions (Coates *et al.* 1994). The rapid increase in logging activity in Alberta since 1992 has magnified the importance of white spruce regeneration, in order to maintain the white spruce component of the mixedwood forest (Lieffers and Beck 1994).

White spruce has a regeneration strategy that relies solely on annual seed production (Nienstaedt and Zasada 1990) because it does not reproduce vegetatively in the southern boreal forest, and lacks a reliable bank of dormant seeds in the soil (Johnson and Fryer 1996, Rowe 1955). Thus, factors that limit the availability of seeds to logged areas, either spatially or temporally, can affect regeneration density and patterns. These factors include white spruce density, annual cone production and seed predation.

White spruce seeds are wind-dispersed, usually falling within 100m of the seed source (Dobbs 1976, Zasada and Lovig 1983). Limited seed dispersal capability and complete dependence on seeds for regeneration makes the density and dispersion of white spruce seed sources an important consideration for forestry companies wanting natural regeneration in cutblocks. Retaining white spruce seed trees within cutblocks is an approach to mixedwood management that promotes regeneration through natural re-seeding (Lieffers and Beck 1994, Lyon and Robinson 1977). The seed tree harvesting method was introduced in the mixedwood forest of northern Alberta in 1950 (Lees 1963). Seed predation is one of the main potential limitations on the success of this regeneration method. However, the role of predators in reducing white spruce seed rain and recruitment in seed tree cutblocks has not been addressed.

White spruce has many natural pre-dispersal seed predators including insects, birds, and the North American red squirrel (*Tamiasciurus hudsonicus*). Insects that

commonly damage the seeds of white spruce include spruce seed worms (*Cydia youngana*), spruce cone maggots (*Hylemya anthracina)*, spruce coneworms (*Dioryctria reniculelloides*), spruce seed midges (*Mayetiola carpophaga*) and seed wasps (*Megastigmus atedius*) (Miller 1986, Ruth *et al.* 1982). Seed losses to insects can vary dramatically among sites and years, ranging between 4 and 100% seed loss (Miller 1986). Insect predation was not the focus of the current study, and was not quantified.

Birds in the Families Paridae (black-capped and boreal chickadees), Sittidae (red-breasted nuthatch), and Fringillidae (red and white-winged crossbills, pine siskins, pine grosbeaks) consume seeds from cones of the genus *Picea* in the mixedwood forest (Fisher and Acorn 1998, Halvorson 1986). Most birds will not store cones, and are therefore confined to extracting seeds during the brief time period between cone opening and seed dispersal. Damage to cone crops by birds is only sporadic and local, and evidence of this is largely anecdotal (Halvorson 1986).

Red squirrels are the primary and most effective vertebrate cone predator of white spruce because of their efficiency in cutting cones (Halvorson 1986). They inhabit coniferous and mixedwood forests across North America, depending on conifer seeds for overwinter survival (Rusch and Reeder 1978, Smith 1968a). White spruce seeds are preferred over black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) (Brink and Dean 1966, Rusch and Reeder 1978), and are the major constituent of a squirrel's diet when available (Smith 1968b). Squirrels cut cones from white spruce trees in late summer and early fall, after seeds are mature but before they are dispersed. By harvesting cones from white spruce seed trees and trees in the forest adjacent to cutblocks, squirrels reduce the density of seed rain in cutblocks.

Red squirrels do not effectively disperse seeds of white spruce. Caching cones in underground tunnels keeps cones cool and moist, preventing them from opening and releasing seeds (Vander Wall 1990). Almost all seeds in cached cones lose their viability after 1 to 2 years (Nienstaedt and Zasada 1990). Seeds that escape consumption fall on the accumulation of old cone bracts and organic debris (called a midden) from years of stripping cones near their cone cache. This organic seedbed is unsuitable for white spruce seed germination (DeLong *et al.* 1997, Nienstaedt and Zasada 1990). No spruce seedlings

were found on squirrel middens (*pers. obs.*, Brink and Dean 1966). Since no recruitment is expected from cones that are harvested by squirrels, their foraging directly reduces the availability of white spruce seeds for regeneration.

Red squirrels are territorial central-place foragers (Vander Wall 1990). At the centre of each territory is a large midden which serves as a feeding and cone-cache site (Larsen *et al.* 1997), and from which squirrels make foraging forays for cones. The most efficient way of storing and defending cones is for each squirrel to harvest cones within a circular area and carry them to its midden for defense and storage (Smith 1968a). Territory boundaries are consistent from year to year (Price *et al.* 1986), and contain the minimum area required to sustain squirrels in years of low cone production (Rusch and Reeder 1978). Cutblocks with different levels of seed tree retention represent an experimental manipulation of the cone crop available within squirrel territories. It is important to understand how logging affects the proportion of cones that squirrels will harvest from seed trees by altering the food base for squirrels.

White spruce cone production varies widely across years and is therefore an important variable in understanding natural regeneration patterns. High cone crops (mast years) usually occur every 2 to 6 years, with intervening periods of low or virtually no cone production (Coates *et al.* 1994, Nienstaedt and Zasada 1990). Masting has evolved in many tree species that are vulnerable to continuous, heavy pre-dispersal seed predation (Silvertown 1980). Janzen (1971) hypothesized that mast years would periodically satiate seed predators, leaving enough seeds for regeneration ("predator satiation hypothesis"). Research on pre-dispersal seed predation of Norway spruce (*Picea abies*) (Brockerhoff and Kenis 1996 & 1997) and oak (*Quercus robur*) (Crawley and Long 1995) provides empirical evidence that predator satiation increases the probability that seeds will survive in mast years. There is limited empirical evidence that predator satiation might function in this way for white spruce (Dale *et al.*, in press, Silvertown 1980, Waldron 1965).

The relationship between white spruce seed production and seedling recruitment is complicated by different germination rates on different seedbed types. Disturbed mineral seedbeds are favorable for white spruce recruitment, whereas undisturbed organic soil results in poor recruitment (DeLong *et al.* 1997, Nienstaedt and Zasada 1990). Forest

managers commonly use mechanical scarification to expose mineral soil in order to increase regeneration after logging (Lees 1963, Quaite 1956). However, predators are more likely to limit regeneration on mineral soil because a high proportion of seeds they consume would have potentially germinated. Thus, the availability of mineral seedbed is an important consideration in unraveling the relationship between seed production, predation and recruitment.

The primary objective of the work described in this chapter was to quantify the magnitude of squirrel cone harvests from white spruce trees, in a year of moderate cone production, and to determine patterns of cone harvesting in cutblocks varying in percent spruce retention, seed tree density and spatial arrangement. Without empirical data on squirrel cone harvesting of white spruce in a similar test system or the knowledge of how large the squirrel population was, I could only make the general prediction that squirrels would harvest a significant proportion of the cone crop of white spruce trees in a non-mast year.

As a component of the primary objective, I compared the proportion of cones harvested by red squirrels from seed trees within cutblocks to that harvested from trees in the adjacent forest (referred hereafter to as control trees). Based on squirrel foraging behaviour, I expected they would harvest cones from seed trees left in their territory after logging, rather than increase their travel distance by making forays to the forest edge, or relocating their territory to the forest. I predicted that seed trees would have a greater proportion of their cones harvested than control trees, as the squirrels attempted to compensate for the trees removed from their territories through logging. The predator satiation hypothesis (Janzen 1971) suggests an inverse relationship between cone abundance and the magnitude of pre-dispersal seed predation. Thus, my second prediction was that, within the range of seed tree retention tested, the proportion of cones harvested from seed trees would increase as retention levels decreased. Both predictions assume that the range of spruce retention levels tested were above the threshold level necessary for squirrels to hold territories and survive in the cutblocks.

METHODS

Study sites

I studied pre-dispersal seed (cone) predation of white spruce during the fall of 1998 in logged areas of the Mid Boreal Mixedwood Ecoregion of Alberta (Strong and Leggat 1992). This region is characterized by stands of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) mixed with white spruce (*Picea glauca*). Poorly drained areas are dominated by black spruce (*P. mariana*), while well-drained areas are dominated by jack pine (*Pinus banksiana*) (Strong and Leggat 1992).

The research was conducted in eight cutblocks within the Forest Management Agreement area of Alberta Pacific Forest Industries Inc. in northeastern Alberta (Township 71 Range 13, W4; 55° 08′, 111° 55′). Five of these cutblocks were harvested in summer 1997 (cutblocks 4-8) and three in winter of 1997-1998 (cutblocks 1-3) (Table 2.1). Average cutblock size was 18.9 ha, ranging from 9.6 to 35.5 ha (Table 2.1). Average seed tree density was 19.4 trees/ha, ranging from 2.6 – 48.5 trees/ha. Seed trees were retained in each cutblock as single trees or patches, ranging in size from 2 trees to islands of more than 50 trees. Patches were composed solely of white spruce, or a mix of white spruce and deciduous trees.

To determine the proportion of the pre-logging volume of white spruce retained as seed trees in each cutblock, I summed the individual seed tree volumes and divided that by the volume of spruce removed through logging plus the volume of seed trees retained. Individual volumes of seed trees were determined using the "Ecologically based Individual Tree Volume Tables for White Spruce (*Picea glauca*)" for the central mixedwood region of Alberta (Huang 1994), which gives volume based on diameter at breast height and tree height. The seed trees in the cutblocks represented between 4.9 and 54.2 % retention of pre-harvest spruce volume (Table 2.1).

The pre-logging canopy cover was aspen-dominated in seven cutblocks, and an equal white spruce-aspen mix in one cutblock (Table 2.2). The canopy cover of the adjacent forest matrix was trembling-aspen dominated in four cutblocks, white spruce dominated in one cutblock, an equal white spruce-aspen mix in two cutblocks, and black spruce dominated in one cutblock (Table 2.2). Balsam poplar and paper birch (*Betula*

Table 2.1: Characteristics of experimental cutblocks used to study red squirrel cone-harvesting from white spruce trees. Large seed tree patches were defined as having ≥ 20 trees; small patches had 2 – 19 trees.

Cutblock (#)	Size (ha)	Total Seed Tree Density (#/ha)	Seed Trees in Patches (%): Large	Small	Singles	Spruce Retention (% volume)
1	9.62	48.53	4	15	81	54.2
2	23.54	9.56	6	5	89	27.8
3	11.16	13.44	25	52	23	5.0
4	10.43	37.89	59	28	13	17.6
5	35.47	2.59	40	17	43	4.9
6	21.18	8.97	45	26	29	11.0
7	11.33	9.53	38	29	33	16.3
8	28.53	24.99	81	9	10	13.2

Table 2.2: Canopy cover of tree species with >5% cover in each cutblock (before logging) and adjacent forest. Values derived from Alberta Vegetation Inventory harvest plan map of Township 71, Range 13.

Cutblock (#)	Cutblock (% canopy cover) Sw*	Aw	Other	Forest (% canopy cover) Sw	Aw	Other
1	5	65	20 (Bp), 10 (Pb)	5	80	5 (Bp), 10 (Sb)
2	20	75	5 (Sb)	15	85	0
3	50	50	0	35	55	10 (Sb)
4	5	80	10 (Pb), 5 (Sb)	5	10	85 (Sb)
5	30	70	0	50	50	0
6	20	80	0	50	50	0
7	5	95	0	80	20	0
8	40	60	0	25	70	5 (Sb)

* Species: Sw = white spruce, Aw = trembling aspen, Bp = paper birch, Pb = balsam poplar, Sb = black spruce; species with < 5% cover omitted

papyrifera) were present in two cutblocks (pre-logging) and one forest matrix. Patches of black spruce were also occasionally interspersed in some cutblocks (pre-logging) and forest matrices. Canopy cover values in Table 2.2 were determined using crown closure data (to the nearest 10%) from the Alberta Vegetation Inventory harvest plan map of the township. Canopy cover values from polygons in each cutblock or forest matrix were weighted according to the proportion of area they covered. The total canopy cover for each species is presented.

Quantification of cone harvest

i) cone photographs

I quantified squirrel cone harvesting by comparing the number of cones on photographs of individual trees before and after cone harvesting. Since squirrels do not effectively act as dispersal agents, this provided a direct estimate of the proportion of cones (seeds) no longer available for regeneration. White spruce cones are not serotinous, so most cones fall off overwinter. Thus, I was able to quantify predation on the 1998 cone crop only.

The pre-caching cone crop on each tree was quantified between 7 July and 28 July 1998. This was before I observed squirrels caching cones (caching commences early August in Alaska, Smith 1968b), but after new cones had reached their full size (*pers. obs.*, Nienstaedt and Zasada 1990). I photographed the cone-bearing portion of approximately 50 white spruce seed trees within each cutblock and 50 trees in the forest adjacent to each cutblock (control trees). In each cutblock, I selected seed trees from across the entire cutblock area, and representative of all spatial arrangements (singles to large patches). Selection was also based on having a clear view of the tree crown for the photograph. Control trees in the uncut forest were usually located within 50m (but up to approximately 80m) of the cutblock edge. There is no difference in white spruce cone production between trees at the forest edge and those in the forest interior (S. Pelech, *pers. comm*). I quantified cone harvests from seed and control trees because they represent important seed sources for cutblocks. This also allowed me to compare harvesting by squirrels with variable proportions of their food base removed through logging versus that by squirrels with an unaltered food base (uncut forest).

Photographs were taken with a 300mm telephoto lens mounted on a tripod, using Kodak 100 ISO and Kodak 200 ISO film. I recorded the compass bearing of each pre-caching photograph, so post-caching photographs could be taken from the same direction. Each tree was individually numbered for subsequent identification.

Between 25 August and 22 September, 1998, I monitored cone-clipping by ten different squirrels in the study area to ensure cone-clipping had ceased before post-caching photographs were taken. A total of ten squirrel middens were located in the forest adjacent to two cutblocks. The number of newly clipped cones was counted and removed from four plots ($1m^2$) near each of the ten squirrel middens. This was done three times at roughly two-week intervals. These data are a minimum index of squirrel cone harvesting, as some newly clipped cones in the plots may have been retrieved and transported to the midden in the intervening period between cone counts. I calculated the overall decrease in cone-clipping by comparing the highest mean number of cones in each plot with the number of cones at the last visit, when few clipped cones were found. Cone-clipping decreased by 91% in my plots before post-caching photographs were taken (Figure 2.1).

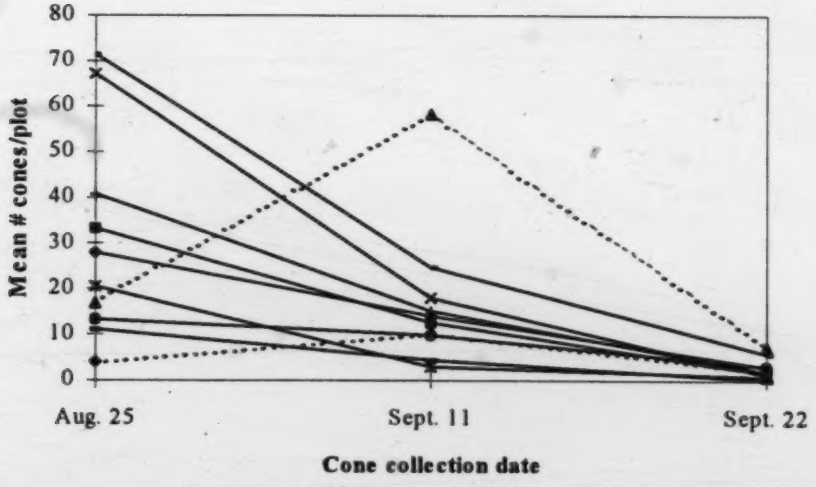

Figure 2.1: Mean number of white spruce cones collected on different dates between 25 August and 22 September, 1998. Cones were collected from four $1m^2$ plots near each of ten squirrel middens. A total of 40 plots were monitored to determine when cone-caching had ceased. Dashed lines differentiate two squirrels with late caching peaks.

I took post-caching photographs between 29 September and 19 October 1998. Pre-caching photographs were taken into the field to ensure that each tree was re-photographed from the same direction and approximate distance. Photographs were developed as 10cm x 15cm prints. With the aid of a magnifying lens, I counted the number of cones on pre- and post-caching photographs of each tree, in order to calculate percent cone loss. Poking a hole in each cone ensured that cones were not missed or counted more than once on photographs.

ii) harvesting from single seed trees vs. large patches

I compared the average proportion of cones harvested from a subsample of 50 seed trees retained as singles and 68 retained in patches of twenty or more trees. The number of trees selected from each cutblock was roughly proportional to the representation of singles and large patches in each cutblock. The large patches were usually dominated by white spruce, or a mixture of spruce and aspen.

iii) ratio of cone crop estimate to actual cone crop

I determined the relationship between cone crop estimates from photographs and the actual cone crop on the trees. The number of cones was counted on 20 felled trees in July 1999, and regressed against cone crop estimates from photographs of the tops of the same trees. Cone crops estimates from photographs were obtained using the same methods described above.

Seed rain density[1]

Seed traps ($0.25m^2$) were placed in a uniformly spaced grid pattern across each cutblock. Forty traps were placed in each of six of the eight cutblocks, and twenty were placed in cutblock 1. No traps were used in cutblock 4. Traps were put out in the spring of 1998, before the beginning of seed dispersal, and collected in November, after most seeds had been dispersed. Traps were constructed with a mesh size that allowed white spruce seeds to enter, but not large enough to allow access to small mammals or birds. The bottoms were constructed with insect screening to allow moisture to escape. Traps were elevated approximately 25cm above the ground.

[1] Seed rain data were supplied by Alberta Pacific Forest Industries Inc.

Squirrel abundance

I used squirrel call surveys to determine the relative abundance of squirrels within each cutblock and adjacent forest. Call surveys were done between 24 May and 4 June 1998, before juveniles emerge from the nest and disperse in search of a territory and begin territorial calling (M. Wheatley, *pers. comm.*; Rusch and Reeder 1978). Therefore, 1998 juveniles were not included in my estimation of squirrel abundance. It is likely that some juveniles obtained territories in the study area (Larsen and Boutin 1994), so the results of my surveys are a conservative estimate of abundance. Without specific knowledge of how differences between study sites would affect patterns of juvenile dispersal, I assumed that the possible underestimate of squirrel abundance was equal across all study sites.

Call stations were located at intervals of 100m around the periphery of each cutblock, at which points squirrel calls were recorded for five minutes. I estimated the number of individuals per call station by recording successive calls from the same location as one individual squirrel. Calls from squirrels within the cutblock and adjacent forest were recorded separately at each station. Territorial "rattles" (Lair 1990), indicative of the presence of a resident squirrel, were the only calls used to estimate squirrel abundance. Surveys were conducted between 6AM and 10AM, when most calling occurs. Surveys were not done during inclement weather, as this decreases the frequency of calling (Smith 1968a). Each cutblock was surveyed on three different mornings, with different observers on consecutive mornings to minimize observer bias. The number of squirrels at each call station was averaged across all three surveys. The number of squirrels at each call station was averaged across all call stations in that cutblock, to provide a measure of relative abundance of squirrels (#/call station) within each cutblock and adjacent forest.

Data analysis

i) white spruce cone crop in 1998

To estimate the actual cone crop of white spruce trees in 1998, I regressed the number of cones counted on photographs of the 20 felled trees against the actual number of cones counted on those trees. Cone crop estimates from photographs (dependent variable) and actual cone crop data (independent variable) were log transformed to improve homoscedasticity and the linearity of the relationship (Sokal and Rohlf 1981).

Based on the line of best fit equation: $Y = mx + b$, I predicted the log actual cone crop (log X) from the log estimated cone crop (log Y) of each sampled tree using the equation for inverse predictions: $\log X = (\log Y - b)/m$ (Sokal and Rohlf 1981).

ii) magnitude of squirrel cone harvests

To determine whether the number of cones on white spruce trees was significantly lower after squirrel cone harvesting, I compared the number of cones counted on pairs of pre-and post-caching photographs of individual trees. The distribution of the differences between pre- and post-caching cone counts was positively skewed for seed and control trees in each cutblock, breaking the assumption of normally distributed differences between pairs of data. Thus, I chose to use non-parametric Wilcoxan paired-sample tests on the cone count data from each cutblock, rather than paired T-tests.

To test the prediction that the proportion of cones harvested from seed trees would be higher than that of control trees at each cutblock, I performed a Mann-Whitney test on the data from each cutblock. The proportion of cones harvested from my sample of seed and control trees at each cutblock were not normally distributed (even when arcsine transformed), so the assumptions of the parametric T-test were not met.

iii) factors affecting squirrel foraging

Four independent variables were measured for each cutblock: percent seed tree retention, seed tree density, percent of seed trees retained in patches of more than 20 trees, and relative squirrel abundance. To test whether these variables contributed significantly to the variation in the average percent of cones harvested from seed trees in each cutblock they were entered into a forward selection stepwise multiple regression model, with an entry criterion of $p = 0.05$. Percent data were arcsine transformed to meet the assumption of a normal distribution (Zar 1996).

This model allowed me to test my prediction that the average proportion of cones harvested would increase as the percent of white spruce retention decreased. Percent retention was used in this analysis because it is a measure of the amount of spruce still available to squirrels in their territory, relative to what was there before logging. Seed tree density is an absolute measure of food availability to squirrels in the cutblocks. It was used in this analysis to provide information to forest managers regarding how patterns of

cone loss related to seed tree density. Seed tree density is a variable that forest managers can manipulate to increase recruitment density.

In order to assess the impact of spatial arrangement on the percent of the cone crop harvested from seed trees, I performed a two-sample t-test on the percent cone loss data from the sample of seed trees retained as singles versus those in large patches. The results of this analysis indicated that spatial arrangement of seed trees affected squirrel foraging patterns. Therefore, I included the proportion of seed trees in large patches in each cutblock in the multiple regression model, to see if this affected overall mean cone loss.

Relative squirrel abundance varied among cutblocks, and between each cutblock and adjacent forest. To determine if squirrel abundance explained the average proportion of cones harvested from seed trees, I included the relative abundance of squirrels at each study site in the multiple regression model. I also performed a simple linear regression of the average proportion of cones harvested from control trees adjacent to each cutblock and the relative abundance of squirrels.

To test if the size of the cone crop of individual trees affected squirrel cone harvesting, I regressed the percent of cones harvested from each tree on the pre-caching cone count. Percent data were arcsine transformed to approximate a normal distribution.

iv) seed rain density

I regressed the mean density of seed rain on the density of seed trees in each cutblock. This allowed me to determine if, despite squirrel foraging, seed rain density increased as seed tree density increased, within the range of tree densities tested. All statistical tests were performed using SPSS (Version 7.5) at a significance level of $p \leq 0.05$.

RESULTS

White spruce cone crop in 1998

White spruce cone production in the study area in 1998 was visually rated as moderate, with many cones on 25-50% of trees (rated 5 out of 7, following Eremko *et al.* 1989). Before squirrels cached cones, cone-bearing trees had an average of 416 ± 21 cones (95% confidence interval, n = 655 trees) visible in photographs of tree tops (Table

2.3). The regression of estimated number of cones (from photographs) on the actual number of cones counted on the trees was highly significant (Figure 2.2). The actual number of cones on white spruce trees in 1998 was, therefore, calculated as 1733 $\pm$ 278 cones, averaged across seed and control trees in all eight cutblocks.

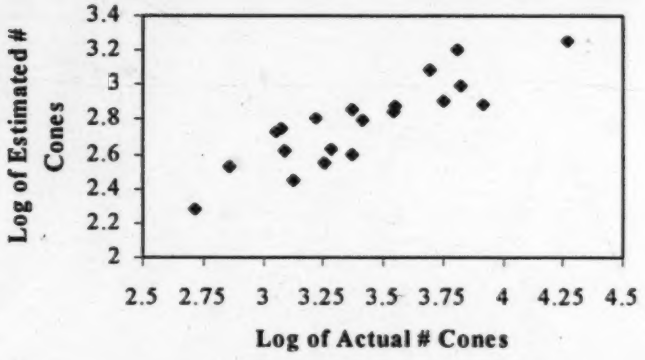

Figure 2.2: The relationship between the log of estimated number of cones counted on photographs of white spruce trees and the log of actual number of cones counted on the same trees after they were felled. Regression line: logY = 0.556 (logX) + 0.882. Linear regression was significant ($R^2 = 0.767$, $p < 0.001$, df = 19).

Table 2.3: Mean number of cones counted on photographs of white spruce trees before ("pre") and after ("post") cone-harvesting by red squirrels. Seed trees were retained within cutblocks and control trees were in the adjacent forest. Sample sizes are the number of trees photographed in each cutblock. P values are from Wilcoxan paired sample tests.

	Seed trees				Control trees			
Cutblock	Sample size	Mean # cones			Sample size	Mean # cones		
(#)	(n)	Pre	Post	p value	(n)	Pre	Post	p value
1	59	362	204	<0.01	39	400	183	<0.01
2	48	490	277	<0.01	45	537	240	<0.01
3	30	379	284	<0.01	34	367	183	<0.01
4	21	286	206	<0.01	43	302	154	<0.01
5	39	465	245	<0.01	52	442	201	<0.01
6	51	354	191	<0.01	44	489	201	<0.01
7	6	551	306	0.014	51	446	168	<0.01
8	45	424	171	<0.01	48	392	146	<0.01

Squirrel cone harvests

i) cutblocks

Squirrel cone harvesting resulted in a significant decrease in the number of cones counted from pre- to post-harvest photographs for both seed and control trees at all cutblocks (Wilcoxan paired sample tests; Table 2.3). The mean percent of cones harvested by squirrels from seed trees ranged from 29.5% (cutblock 3) to 54.6% (cutblock 8), with an overall mean of 42.7% (Figure 2.3). The mean percent of cones harvested from control trees ranged from 48.3% (cutblock 3) to 63.1% (cutblock 8), with an overall mean of 55.9% (Figure 2.3). Contrary to my prediction, control trees had a higher proportion of cones harvested than seed trees in all cutblocks. This difference was statistically significant in most cutblocks, except 5, 7 and 8 (Mann Whitney tests; Figure 2.3).

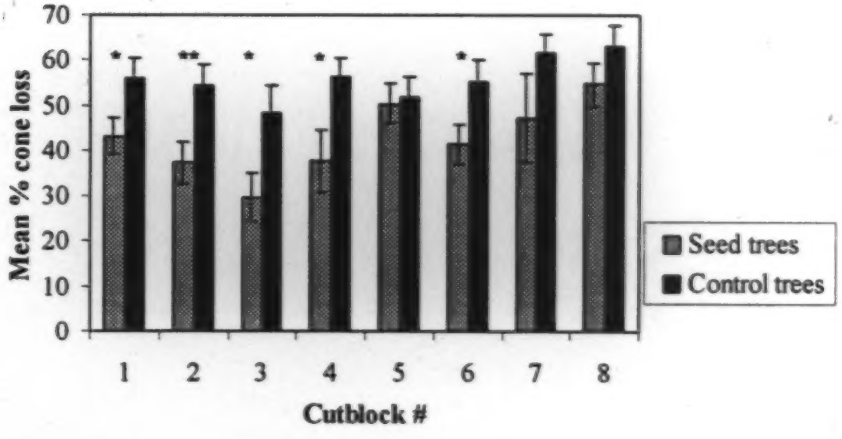

Figure 2.3: Mean percent of cones harvested by red squirrels from seed trees within eight cutblocks and control trees in adjacent forest of each cutblock. Error bars are ± 1 standard error. See Table 2.3 for sample sizes. Mann Whitney tests determined if the proportion of cones harvested was significantly different for seed and control trees at each cutblock. * $p < 0.05$, ** $p < 0.01$

ii) individual trees

Squirrels did not forage equally in all trees. At all study sites, the percent of cones harvested varied widely among trees, ranging from 0-96% and 0-98% per tree in seed and

control trees, respectively. Squirrels did not concentrate their foraging in trees with larger cone crops. I found no significant relationship between the number of cones on trees before cone harvesting and the proportion of cones removed by squirrels from seed trees ($R^2 = 0.003$, $p = 0.319$, $df = 298$) or control trees ($R^2 < 0.001$; $p = 0.806$, $df = 355$). I therefore tested other variables to see if they affected squirrel foraging patterns.

Factors affecting squirrel foraging patterns

i) relative squirrel abundance

Of the four predictor variables included in the multiple regression model, only relative squirrel abundance significantly predicted average percent of cones harvested from seed trees in the cutblocks (Figure 2.4). The total relative abundance of red squirrels within each cutblock plus adjacent forest varied 4.5 fold, ranging from 0.13 and 0.59 squirrels/call station ("Total Abundance", Table 2.4). Total squirrel abundance at each study site was also positively related to the mean percent of cones harvested from control trees ($R^2 = 0.589$, $p = 0.028$, $df = 7$).

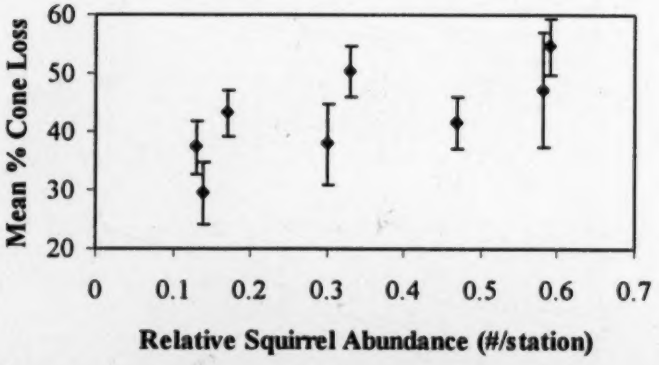

Figure 2.4: The relationship between mean percent cone loss from seed trees and total relative abundance of red squirrels at each study site ($R^2 = 0.525$, $p = 0.042$, $df = 7$). Relative abundance was measured as the number of squirrels per call station, located at 100m intervals along the periphery of each cutblock. Error bars are $\pm$ 1 standard error. See Table 2.3 for the sample sizes. $Y = 17.913(X) + 34.652$.

Table 2.4: Relative red squirrel abundance within each cutblock, in the adjacent forest, and both areas combined (total relative abundance). Data from spring call surveys are expressed as the average number of resident squirrels per call station. Call stations were located at 100m intervals around the periphery of each cutblock.

Cutblock #	Within Cutblock (# / call station)	Adjacent Forest (# / call station)	Total Abundance* (# / call station)
1	0.05	0.12	0.17
2	0.03	0.1	0.13
3	0	0.14	0.14
4	0.04	0.26	0.3
5	0.03	0.3	0.33
6	0.06	0.41	0.47
7	0	0.58	0.58
8	0.17	0.42	0.59

*Total squirrel abundance = relative abundance within cutblock + adjacent forest.

Squirrel abundance within cutblocks was on average less than 20% of that in the adjacent forest, ranging from 0 to 0.17 squirrels/call station ("Within Cutblock", Table 2.4). This suggests that either some squirrels abandoned territories in the cutblocks, or they were unable to survive there. Cutblocks 3 and 7 had no resident squirrels recorded within them (Table 2.4). Nonetheless, squirrels harvested 30 and 47% of cones from seed trees in cutblocks 3 and 7, respectively. Cutblock 3 had very low spruce retention (5%), while cutblock 7 had a slightly higher retention level (16.3%), but very low pre-logging spruce canopy cover (5%). Cutblocks 3 and 7 had lower than average seed tree density, and were both below average cutblock size.

ii) seed tree retention and density

Contrary to what I predicted, mean percent cone loss from seed trees did not increase significantly as percent spruce retention decreased, within the range tested (4.9 - 54.2% of pre-logging volume). Mean percent cone loss in each cutblock also was not predicted by seed tree density, within the range tested (2.6 – 48.5 trees/ha). No trend in percent cone loss was evident with either variable. Neither variable was selected for inclusion in the regression model.

iii) spatial arrangement of seed trees

Seed trees in large patches (> 20 trees) had an average of 50.5% of cones harvested (n = 68), while single trees had an average of 33.4% harvested (n = 50). This was a significant difference in the percent of cones harvested (two-sample t-test, p = 0.001). The frequency distribution of the cone harvest data for single seed trees was distinctly right skewed, with 34% of trees having only 0-10% of their cones harvested (Appendix 2.1). In contrast, many (21%) seed trees in large patches had 70-80% of cones harvested (Appendix 2.1). The distribution of cone harvests from trees in large patches resembled that of control trees in the forest adjacent to some cutblocks (Appendix 2.2).

Cutblocks with a higher proportion of seed trees retained in large patches tended to have a higher overall mean percent of cones harvested from seed trees (Figure 2.5). However, the proportion of seed trees in large patches was not a significant predictor of the mean percent of cones harvested from seed trees in the eight cutblocks studied.

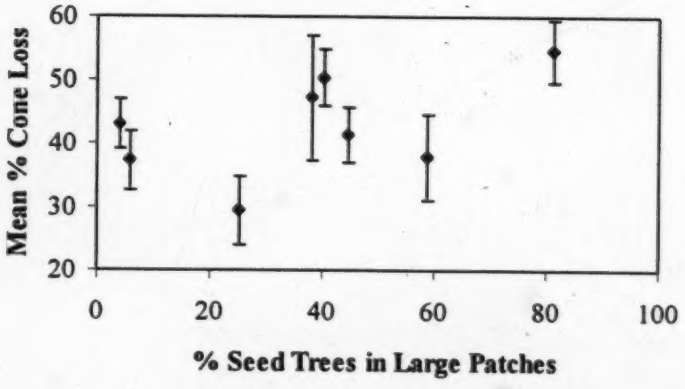

Figure 2.5: The relationship between the mean percent of cones harvested from seed trees and the proportion of trees retained in patches of 20 or more trees in each cutblock. This relationship was not statistically significant (partial $r^2 = 0.02$, $p = 0.757$). Error bars are $\pm$ 1 standard error. See Table 2.3 for the sample sizes.

Natural seed rain in the cutblocks

Average seed rain density in each cutblock, as assessed by seed traps, ranged between 0 and 18.2 seeds/m^2. The number of seeds counted in different traps within each cutblock was extremely variable, a reflection of strong spatial heterogeneity in seed rain. This was especially evident at higher seed tree densities (apparent in the large error bars in Figure 2.6). Seed rain density increased significantly as seed tree density increased, within the range of tree densities tested (Figure 2.6). Thus, despite squirrel foraging patterns, retaining more seed trees resulted in higher seed rain density in the cutblocks studied.

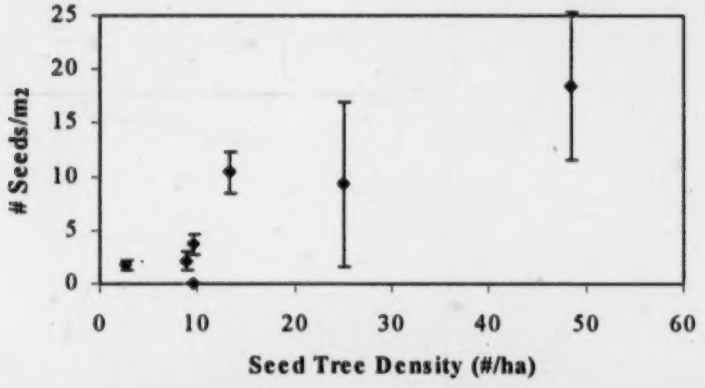

Figure 2.6: The relationship between seed tree density and average seed rain density from seed traps in seven cutblocks ($R^2 = 0.831$, $p = 0.004$, $df = 6$). Forty seed traps were used in six cutblocks, and only 20 were used one cutblock. Error bars are $\pm$ 1 Standard Error. $Y = 0.383(X) + 0.10$.

DISCUSSION

Magnitude of squirrel cone harvests in 1998

Although this study was not conducted in a mast year, only half of all white spruce seeds were depredated by squirrels. Studies in other forest systems have also found that in moderate seed crop years, approximately half of the seeds escape pre-dispersal predation (e.g. Crawley and Long 1995), whereas others have found that relatively few seeds escape pre-dispersal predation in these years (e.g. Dale *et al.*, in press). Halvorson (1986) emphasized that the magnitude of cones harvested by squirrels can vary with factors other than cone crop size, such as weather during cone harvesting season, seed viability, the size

of the squirrel population and the availability of other food sources. Warm, dry weather can speed up the process of cone-drying and seed-shedding (Coates *et al.*1990), shortening the time period during which squirrels can cache cones. Thus, fewer cones may be collected in years of warmer or drier than average weather. Weather in the study area during the fall (August to October) of 1998 was slightly warmer and much drier than average (Environment Canada, Appendix 2.3). Squirrels may have had a shorter time span over which they could collect cones in 1998, reducing the overall magnitude of their harvest in the study area.

Squirrels defend territories that are large enough to provide sufficient seed resources in years of low cone production (Rusch and Reeder 1978). Since this study was conducted in a year of moderate cone production, it is likely that some cones on seed trees within each squirrel territory would be surplus (Smith 1968b). A surplus of cones could provide some squirrels with enough seed resources to remain in the cutblocks, even after a substantial portion of spruce trees were removed from their territory by logging. Smith (1968b) found that squirrels in white spruce habitat in Alaska were able to survive by utilizing excess cached cones in a year of cone crop failure, however, squirrel numbers decreased by 67% following the second consecutive year of cone failure. This study was conducted within one year after logging, so it is possible that cone caches contained enough seeds to sustain squirrels in the absence of enough cone resources. I predict that squirrel abundance in cutblocks will decline following years of low cone production. My data indicate that squirrel abundance was an important predictor of the magnitude of cone harvests. By repeating the research described in this chapter over years of variable cone production, one could determine how the magnitude of squirrel cone harvests is affected by time since logging, the size of the cone crop and squirrel population fluctuations. This would also allow determination of whether seed trees are more heavily relied upon for seed resources in years of low cone production, or whether reduced squirrel abundance in cutblocks in these years results in lower cone harvests.

Cone harvesting patterns

Seed trees had an average of 43% of their cones harvested by squirrels. I had predicted, based on red squirrel foraging and territorial behaviour, that seed trees were

vulnerable to predation if spruce retention was high enough to provide a food base for squirrels to maintain territories in the cutblocks. Red squirrels have been found to be reluctant to relocate their territories to higher quality habitat, possibly because losing familiarity with their territory decreases survival and foraging efficiency (Larsen and Boutin 1994, 1995). Squirrels unable to secure a new territory, and thus without a reliable overwinter cone supply, have a low probability of survival (Rusch and Reeder 1978, Smith 1968a). Resident squirrels were recorded within six out of eight cutblocks, indicating that the seed resources available in these cutblocks were sufficient for some squirrels to maintain their territory there for at least the first year post-logging, instead of relocating to the forest. Seed trees in the two cutblocks with no resident squirrels nevertheless had a substantial proportion of cones harvested. This may indicate that the amount of spruce retained in these cutblocks extended below that necessary for squirrels to hold territories, but enough seed resources were still available for squirrels to make foraging forays from the forest into the cutblock worthwhile. It is also possible that some juveniles secured territories within the cutblocks subsequent to when squirrel call surveys were done.

I predicted that squirrels with territories in the cutblocks would need to harvest a higher proportion of cones from seed trees to compensate for the trees removed from their territory by logging. Harvesting a higher proportion of cones per tree is more efficient than increasing territory size to incorporate more trees, because clipped cones are brought back to the cache in the centre of their territory (Smith 1968a). Increasing territory size to incorporate more seed trees increases travel time and risk of predation due to exposure in logged habitat (Stuart-Smith and Boutin 1995), and unfamiliarity with the habitat (Metzgar 1967). Price *et al.* (1986) found that squirrels did not increase territory boundaries after the removal of neighboring territory holders. They postulated that one reason for this was that boundaries are set based on the area that squirrels can harvest from efficiently.

Contrary to my prediction, however, the average proportion of cones harvested from seed trees was approximately 15% lower than from control trees in the adjacent forest. One likely explanation for this was the lower squirrel abundance within the cutblocks than the forest. Squirrel abundance was a significant predictor of the average

percent of cones harvested from seed trees at each study site, providing direct evidence of the influence of squirrel abundance on the magnitude of cone harvests.

The lower cone loss from seed trees was also a reflection of the adjustment of foraging behaviour in cutblocks. Squirrels harvested an average of 51% of cones from seed trees in large patches (> 20 trees), but only 33% from single seed trees. There is no strong evidence in my data that squirrels in cutblocks with mostly single trees were more likely to abandon their territories, since the two cutblocks with no resident squirrels (column 2, Table 2.4) had below average proportion of seed trees retained as singles (Table 2.1). Since the distribution of cone loss data from trees in large patches more closely approximated the distribution of cone loss from control trees (Appendix 2.1 and 2.2), it seems that squirrels adjusted their foraging behaviour when single trees were in their territory. Squirrels seemed to avoid foraging in single trees, as many single trees had no cones harvested (Appendix 2.1a). Thus, the presence of single seed trees (and possibly trees in small patches, but this was not tested) reduced the average cone loss of seed trees as compared to control trees.

I did not find evidence in support of my prediction that the average percent of cones harvested from seed trees would vary inversely with the proportion of spruce retained in each cutblock. There are two possible explanations for this. First, my analysis was done at the wrong spatial scale (cutblock versus territory) to reveal a foraging pattern. A more accurate assessment of the relationship between seed tree retention and average cone harvests should have been done by determining the proportion of cones harvested in individual squirrel territories (0.24 - 0.8 ha in white spruce- and aspen-dominated habitat; Rusch and Reeder 1978, Kemp and Keith 1970) containing a range of spruce retention levels. Sanders (1983, *In* Halvorson 1986) found an inverse relationship between cone abundance and the proportion of cones harvested within individual squirrel territories, but no correlation between cone crop size in the study area and the proportion of cones harvested. The proportion of spruce retained within a territory may be more important to a squirrel than the average spruce retention across the entire cutblock, especially if the trees are unevenly dispersed across the cutblock.

My second explanation for the lack of relationship between the percent of cones harvested and spruce retention level is that the spatial arrangement of seed trees (e.g. large patch versus single tree) affected cone harvesting patterns from individual trees. Seed trees retained in large patches may have had more cones harvested than single trees because spruce trees retained in patches provide an efficient food base from which to forage, as well as nesting habitat, and shade for cone caches (Vahle and Patton 1983). Since the spatial arrangement of seed trees varied widely in each cutblock, this may have disrupted any possible relationship between seed tree retention and average cone loss.

Cutblocks with a higher proportion of seed trees retained in large patches tended to have a higher average percent of cones harvested from seed trees than cutblocks with a low proportion of trees in large patches. However, this relationship was not statistically significant. It is possible that the sample of seed trees included in my calculation of average percent of cones harvested from seed trees in each cutblock was not an accurate (proportionate) representation of the spatial arrangement of the seed tree population. Since I did not know the actual proportion of the seed tree population retained in large patches versus singles before I sampled, I may have over- or under-represented trees in large patches in my sample in each cutblock. This may have obscured the relationship between the average cone loss from seed trees and the proportion of trees in large patches. As well, with only eight cutblocks used in the regression analysis (df = 7), my power to detect a relationship was less than 0.5.

Conclusions and management implications

In a year of moderate cone production, approximately half of all white spruce cones produced were lost to red squirrels. Red squirrels harvested an average of 43% (30 – 55%) of cones from seed trees and 56% (48 – 63%) from spruce trees in the forest adjacent to eight cutblocks. Lower squirrel abundance and adjusted foraging behaviour in cutblocks (squirrels avoided foraging in single seed trees) likely explain lower cone harvests from seed trees. Red squirrel abundance was the strongest predictor of the average percent of cones that was harvested from seed trees in each cutblock. Seed tree density and percent spruce retention in cutblocks did not predict the average percent of cones harvested from seed trees in the cutblocks studied.

The average percent of cones harvested from seed trees in each cutblock tended to increase as the proportion of seed trees retained in large patches increased, however this was not statistically significant, based on the eight cutblocks studied. Seed trees in patches of more than 20 trees had a significantly higher proportion of cones harvested (51%) than single trees (33%). Natural seed rain density (assessed with seed traps) increased linearly with seed tree density, however it was highly spatially variable.

Based on these data, forest managers should avoid retaining seed trees in large islands of twenty or more trees. This will minimize squirrel cone harvesting from seed trees, and increase the number of seeds each tree can contribute to regeneration. For the same investment of merchantible timber, well-dispersed seed sources should be more effective at regenerating the adjacent cutblock than fewer large patches because of reduced cone harvesting by squirrels, and more even dispersal of seeds across the cutblock (McClanahan 1986). However, higher susceptibility to windthrow of single trees (*pers. obs.*) is another factor that should be considered when planning the spatial arrangement of seed trees.

If squirrel foraging patterns do not change at tree densities outside the range tested, forest managers should compensate for cone harvesting by leaving a higher density of seed trees. However, patterns of post-dispersal predation of white spruce seeds (Chapter 3) should also be considered when planning cutblocks to achieve regeneration standards through natural re-seeding.

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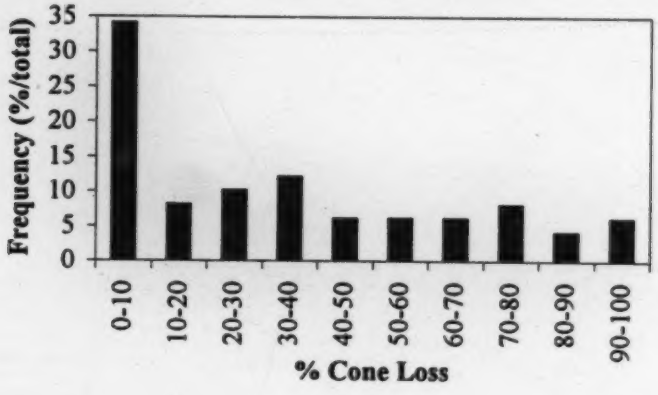
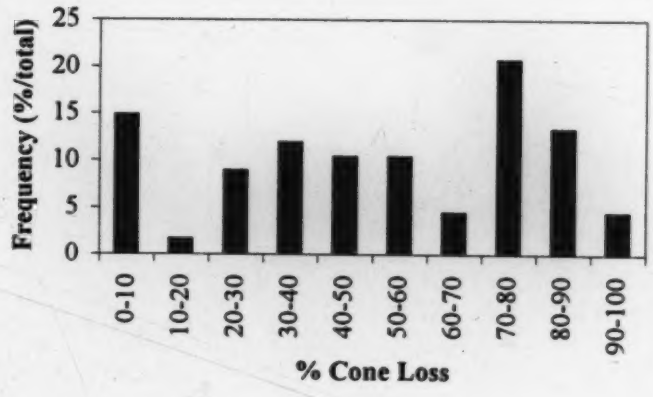
Appendix 2.1: Distribution of the percent of cones harvested from: a) single seed trees (n = 50); and b) seed trees in large patches of more than 20 trees (n = 68). Trees were selected from within eight different cutblocks.

(a)



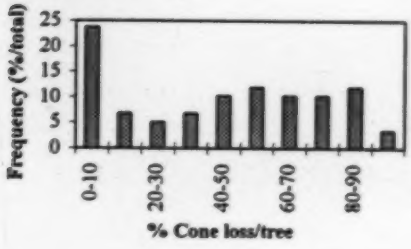
(b)



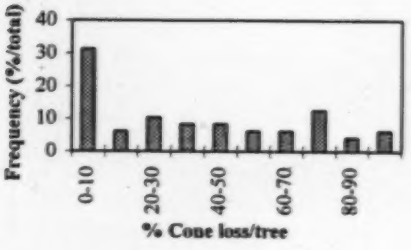
Appendix 2.2: Frequency distributions of percent cone loss data for all seed trees and control trees

Seed trees:

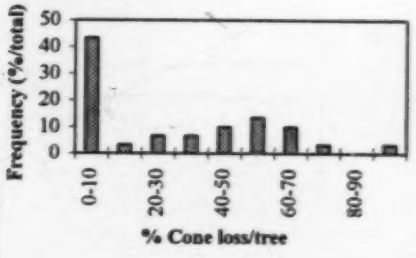
Cutblock 1 (n = 59)



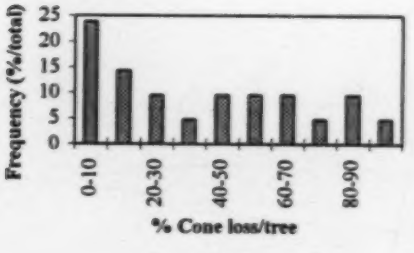
Cutblock 2 (n = 48)



Cutblock 3 (n = 30)

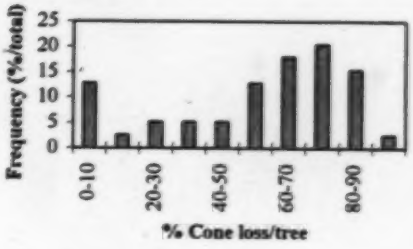


Cutblock 4 (n = 21)

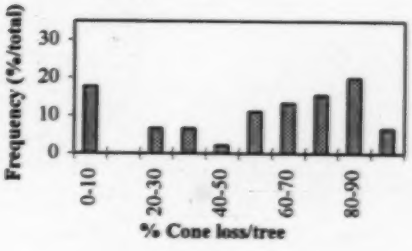


Control trees:

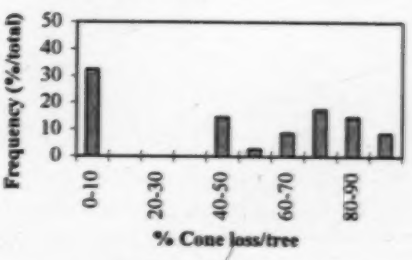
Cutblock 1 (n = 39)



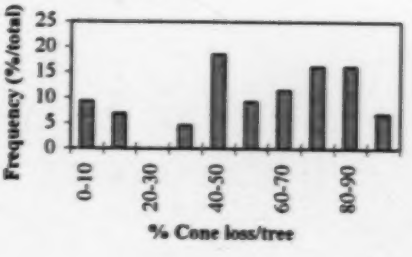
Cutblock 2 (n = 45)



Cutblock 3 (n = 34)



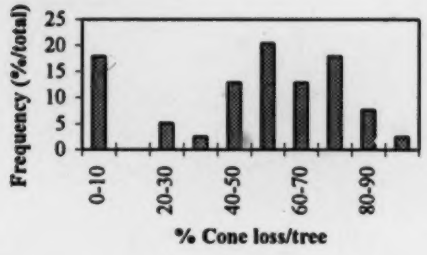
Cutblock 4 (n = 43)



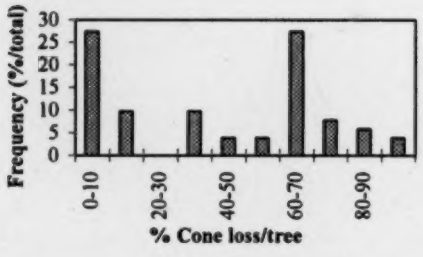
Appendix 2.2 continued:

Seed trees:

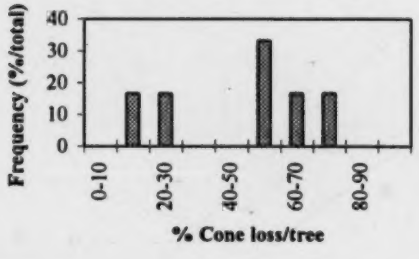
Cutblock 5(n = 39)



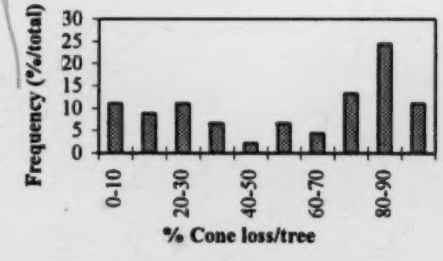
Cutblock 6 (n = 51)



Cutblock 7 (n = 6; Note small sample size)

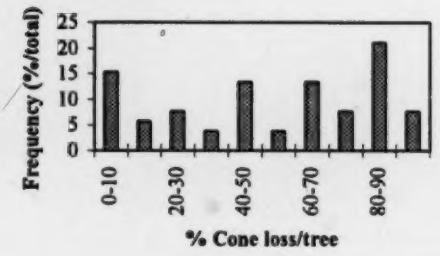


Cutblock 8 (n = 45)

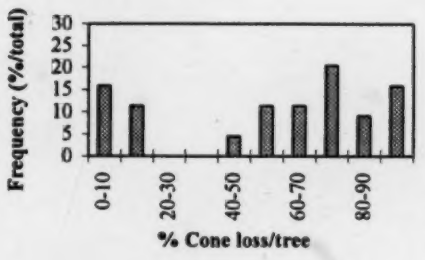


Control trees:

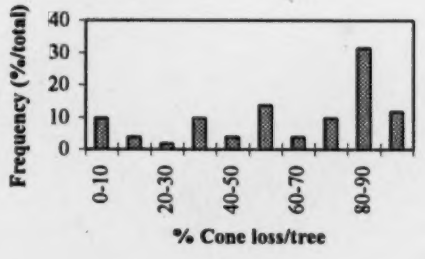
Cutblock 5(n = 52)



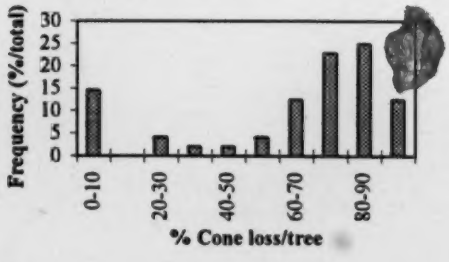
Cutblock 6(n = 44)



Cutblock 7 (n = 51)



Cutblock 8 (n = 48)



Appendix 2.3a: Monthly mean temperature (degrees Celsius) averaged from 1970 to 1997 and for 1998 alone, for Lac la Biche, Alberta*. The study was conducted in 1998.

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1970-1997	-16.7	-12.7	-5.8	3.5	10.1	14.4	16.3	15.1	10.4	3.5	-7.4	-14.4
1998	-19.2	-5.7	-5.2	6.5	13	14.9	17.6	17.5	10.4	4.8	-6.8	-14.1

Appendix 2.3b: Monthly mean precipitation (mm) averaged from 1970 to 1997 and for 1998 alone, for Lac la Biche, Alberta*. The study was conducted in 1998.

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1970-1997	20.5	16.3	18.3	22.4	41.2	83.4	89.8	68.7	45.4	24	20.1	22.4	472.7
1998	17.7	3.9	6.4	17.3	19.6	91.4	78.6	18.8	24.2	26.5	12.6	17.7	334.5

* Lac la Biche, Alberta, is located approximately 50 km south of the study area

Source: Environment Canada

CHAPTER 3

THE EFFECT OF POST-DISPERSAL SEED PREDATION BY SMALL MAMMALS ON WHITE SPRUCE RECRUITMENT

INTRODUCTION

Seedling recruitment involves several processes, from seed dispersal and germination to seedling establishment. Density-dependent or density-independent factors may act and interact at each stage, resulting in a complex relationship between seed rain and recruitment (Houle 1992, 1995). One factor that is important in the transition from seed dispersal to germination is post-dispersal seed predation (Janzen 1971). Foraging by post-dispersal seed predators can alter the abundance and spatial distribution of plants (Schupp 1988, Houle 1992), as well as the species composition and diversity of plant communities throughout succession (Hubbell 1980, Hulme 1996). The effects of seed predation are well-established for many tree species invading old-fields during succession (e.g., DeSteven 1991, Ostfeld and Canham 1993, Myster and Pickett 1993). However, the impact of post-dispersal seed predation on recruitment patterns of white spruce (*Picea glauca*) after logging in the mixedwood boreal forest is not well understood.

Seedling recruitment is crucial for species such as white spruce, which rely on seeds to regenerate after a disturbance (Nienstaedt and Zasada 1990). Seeds of white spruce do not contribute to a persistent seed bank (Johnson and Fryer 1996, Rowe 1955), implying that regeneration comes from dispersed seed. This makes the fate of seed rain critical. Furthermore, regeneration success after logging requires that adequate seed production coincide with the availability of a favorable seedbed for germination, since white spruce has high germination success on mineral seedbed but very low success on organic matter (DeLong *et al.*1997, Nienstaedt and Zasada 1990). Forestry companies use seedbed scarification to expose mineral soil to increase the availability of germination microsites, and ultimately recruitment (Johnson 1973). However, seed predation will have a larger impact on recruitment when germination microsites are not limiting.

The importance of post-dispersal seed predation on white spruce recruitment may vary dramatically among years due to annual fluctuations in seed production that may be 10-fold or more (Nienstaedt and Zasada 1990). The impact of post-dispersal predation

may also vary among years due to fluctuations in small mammal populations. Such fluctuations may be related to food abundance, as shown experimentally for *Clethrionomys* and *Peromyscus* populations by Gilbert and Krebs (1981). Years of high acorn production in oak forests of Poland and eastern United States allow overwinter reproduction and higher survival, resulting in high small mammal densities the following year (Wolff 1996, Pucek *et al.* 1993). Gashwiler (1979) documented fluctuations of *Peromyscus* related to mast crops of Douglas-fir (*Pseudotsuga menziesii*). In one of the few studies to provide evidence of predator satiation in post-dispersal predators, Jensen (1982) reported that rodents consumed only up to 10% of seeds available in a pure stand of beech (*Fagus sylvatica*) in mast years, but up to 100% in non-mast years. There is currently no empirical evidence for a relationship between fluctuations in small mammal populations and white spruce seed abundance in the mixedwood forest of Alberta. Thus, it is unkown whether predator satiation occurs in mast seed years of white spruce. Predator satiation may be less likely in disturbed systems such as cutblocks, due to the reduction in seed availability.

Small mammals are important post-dispersal seed predators in forest ecosystems (Gashwiler 1967, Krauch 1945, Sullivan 1979a). Radvanyi (1966) placed 2000 radio-tagged white spruce seeds in cutblocks and documented their fate, in a year of relatively low small mammal abundance. After 17 weeks, approximately half of the seeds were destroyed, and over 70% of this was due to consumption by deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*). Populations of small mammals generally increase in abundance after clearcutting in North America, although variable responses have been documented (literature review by Kirkland 1990).

The deer mouse occurs across a broad range of habitats (Whitaker 1997), and is associated with large downed woody material in aspen dominated forests (Roy *et al.* 1995). Deer mice are abundant in cutblocks with residual trees and uncut mixedwood forest in Alberta (Weaver 1996, Moses and Boutin, in review). Sullivan (1979a) found that deer mice immediately re-colonized clearcuts in British Columbia. Many studies across a range of forest types found higher deer mouse densities in clearcuts than adjacent forest (Martell 1983, Martell and Radvanyi 1977, Weaver 1996). On the contrary, some

studies have found similar or lower densities of deer mice in clearcut areas than adjacent forest (Monthey and Soutiere 1985, Probst and Rakstadt 1987, Sullivan 1979b).

Red-backed voles are considered forest-dwelling species (Whitaker 1997), associated with shrubs and herbaceous ground cover, snags and coarse woody debris in aspen dominated forests (Roy *et al.* 1995). Yet population increases of red-backed voles have often been documented on recent clearcuts in coniferous and deciduous forests (literature review by Kirkland 1990). They are also able to utilize young clearcuts with residual trees for foraging (Weaver 1996). Martell and Radvanyi (1977) found that red-backed voles were common in the first year after harvesting, but declined thereafter. Retention of residual tree patches may ameliorate negative effects of logging on voles (Moses and Boutin, in review). There are contradictory findings regarding the sensitivity of deer mice and red-backed voles to habitat edges (Sekgororoane and Dilworth 1995, Bayne and Hobson 1998).

Seeds are an important component of the diet of deer mice and, to a lesser extent, red-backed voles. Deer mice feed primarily on seeds, nuts, berries and invertebrates, whereas red-backed voles feed on green herbaceous plants, bark, seeds, nuts, roots, fungi and insects (Hansson 1985, Whitaker 1997). Voles show high variability in their diet, feeding extensively on fungi, lichen and vascular vegetation during summer and fall (Martell 1981, Maser *et al.* 1978, Schloyer 1977). The importance of seeds generally increases in winter when they are relatively more abundant than other food sources (Hansson 1985).

Mice may store some of the seeds that they harvest in small, scattered subsurface caches (Price and Jenkins 1986, Vander Wall 1990). Abbott and Quink (1970) monitored 92 white pine (*Pinus strobus*) seed caches made by white-footed mice (*Peromyscus leucopus*) and red-backed voles, and found that only 3 produced surviving seedlings. They concluded that the contribution of seed caches to forest regeneration was minimal. It is likely that little, if any, recruitment results from white spruce seed caches because the germination microsite is poor, and many caches are recovered due to the highly developed sense of smell of rodents (Howard and Cole 1967, Howard *et al.* 1968).

Ground-feeding birds such as dark-eyed juncos (*Junco hyemalis*), sparrows and chickadees (*Parus* spp.) may also consume spruce seeds (Coates *et al.* 1994), but were not of any consequence in the radio-tagging studies described by Radvanyi (1966, 1970). Predation by birds was not specifically quantified in my research because the methods I used to measure predation did not distinguish the effects of different types of predators.

The objective of this study was to quantify the net impact of post-dispersal seed predation on white spruce recruitment in cutblocks. To achieve this, I sowed seeds into small mammal exclosures (seed mortality due to factors other than predation) and unprotected plots (seed mortality due to predation plus other factors), and compared recruitment density. I manipulated the seed densities used in experimental plots as an attempt to mimic years of high, intermediate and low seed production. I also compared the foraging behaviour of rodents given different seed densities between forest edges and cutblock interiors.

METHODS

Study Sites

I worked in the Mid Boreal Mixedwood Ecoregion (Strong and Leggat 1992) of Alberta, which is characterized by stands of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) mixed with white spruce. Poorly drained areas are dominated by black spruce (*P. mariana*), while well-drained areas are dominated by jack pine (*Pinus banksiana*) (Strong and Leggat 1992). Soils are generally Gray Luvisols or Eutric Brunisols. Mean temperature during the growing season (May to August) is 13.5°C and average annual precipitation is 240cm (Strong and Leggat 1992).

The research was conducted in three cutblocks within the Forest Management Agreement area of Alberta Pacific Forest Industries Inc. of northeastern Alberta (Township 71, Range 13, W4; 55° 08′, 111° 55′). Before harvest, canopy cover of the cutblocks was aspen-dominated with 5 – 30% white spruce canopy cover. The cutblocks were harvested in the summer of 1997, and were an average size of 22.7 ha. An average of 7 trees per hectare (2.6 – 9.5/ha) were retained as seed trees in the cutblocks, representing an average of 11% (5 – 16%) retention of pre-harvest spruce volume.

Approximately half of each cutblock area was mechanically scarified to expose mineral soil in up to 50% of that area. This was done by straight blading with a D6 bulldozer (G. Grover, *pers. comm.*). Canopy cover of the adjacent forest matrix was an equal aspen-white spruce mix in two of the cutblocks, and white spruce dominated in one cutblock.

Recruitment Experiment

I examined the effect of post-dispersal seed predation on white spruce seedling recruitment through an experiment to compare the number of seedlings in areas with seed predation (open plots) to the number of seedlings in comparable areas without seed predation (exclosure plots). I sowed white spruce seeds into each plot at one of three densities. Each replicate consisted of one exclosure with a corresponding open plot for each of the three seed densities (Figure 3.1). I set up three replicates in each of three cutblocks, for a total of nine replicates of each seed density.

i) exclosure design

Exclosures were constructed to prevent access to mice, voles and birds, following some of the guidelines suggested by Wagg (1964). Side panels 30cm in height were constructed with hardware cloth (0.6cm mesh) and supported by a wood frame (2 x 2 inch) and corner posts. Galvanized sheet metal attached to the bottom of the hardware mesh extended 15cm into the ground to prevent access via burrowing by small mammals. Removable lids were constructed with the same hardware cloth and attached with screws. Exclosure plots and open plots were $0.8m^2$, divided in half for spring and fall seed-sowing.

ii) seed sowing

I tested three seed densities within the natural range of white spruce seed rain in the mixedwood forest (literature review in Coates *et al.* 1990, and Nienstaedt and Zasada 1990; J. Stewart, *pers. comm.*): $1000/m^2$ (high, representing a mast year), $400/m^2$ (intermediate), and $100/m^2$ (low). Manipulating seed density allowed me to control the number of seeds in each plot, eliminating the spatial variability and unpredictability of natural seed supply (Leadem 1997).

Cold stratified white spruce seeds were randomly scattered (simulating natural dispersal) in one half ($0.4m^2$) of each exclosure and open plot between 25 and 27 June

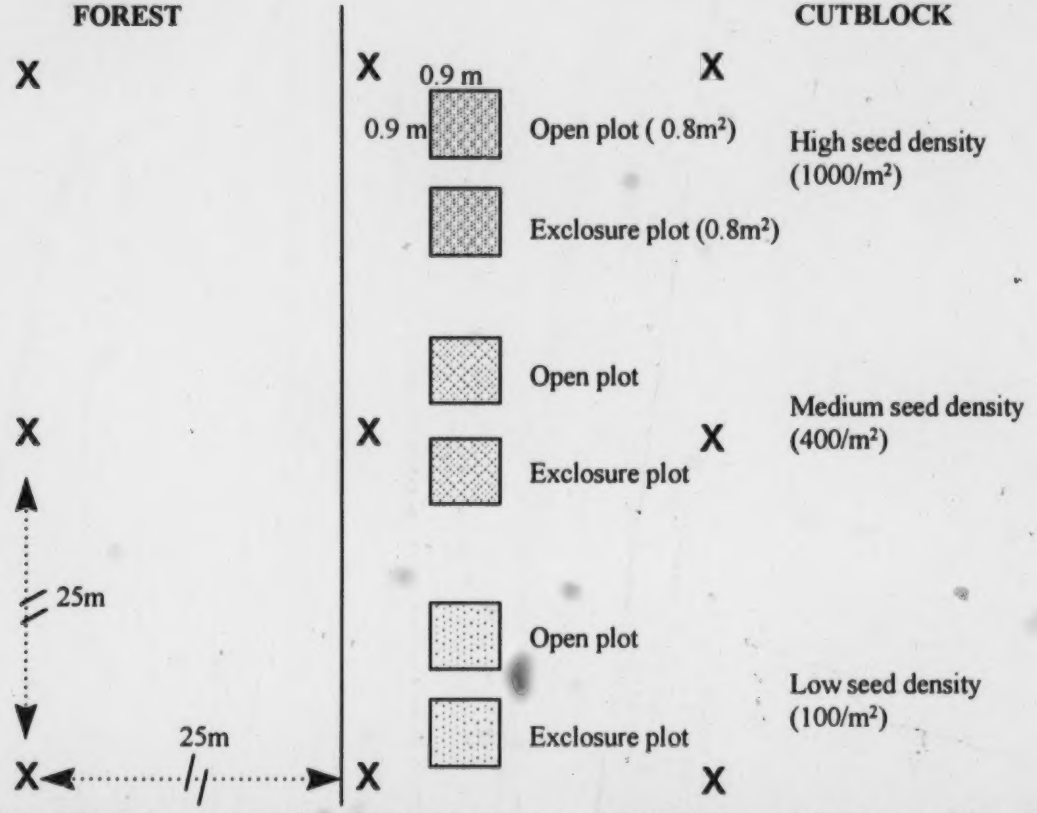


Figure 3.1: Schematic representation of one replicate of recruitment plots, overlain with one 50m x 50m trapping grid. Paired exclosures and open plots were within 2 m of each other, while replicates within the same cutblock were separated by a minimum of 50m. Three replicates were placed in each of three cutblocks, for a total of 9 replicates. Each plot was divided in half for spring and fall seed-sowing. X = location of small mammal trap.

1998. The seeds were cold stratified for 3 weeks at 4°C to mimic natural stratification of seeds that are dispersed in fall and are exposed to cold temperatures overwinter. Seed viability averaged 90% from germination tests using four batches of 100 seeds. The seeds had been collected in 1996 within 36 km of the study area and were obtained from Smoky Lake Forest Nursery, Smoky Lake, Alberta. This first recruitment trial quantified the effect of predation on recruitment over six weeks during the growing season.

White spruce seeds are naturally dispersed in fall (late-August to early November, peaking in September; Coates *et al.* 1994, Nienstaedt and Zasada 1990), and are exposed to predation overwinter until they germinate the following spring. To mimic the natural scenario, non-stratified seeds from the same collection were randomly scattered into the other half ($0.4m^2$) of each exclosure and open plot on 23 September 1998, and exposed to predation overwinter. This second recruitment trial quantified the effect of predation on recruitment over the natural period of seed exposure (approximately nine months).

iii) seedbed conditions

Plots were located on mineral soil within the mechanically scarified area of each cutblock. White spruce has variable germination rates on different seedbed types, with highest germination success on mineral soil (DeLong *et al.* 1997, Nienstaedt and Zasada 1990). I chose to test a mineral seedbed, as this is where white spruce was most likely to be seed- or predator-limited, and the conditions under which seed predation would likely have the largest impact on recruitment. I also wanted to provide information regarding the effects of seed predation in cutblocks with seedbed scarification, as this is a commonly used technique to increase regeneration of white spruce.

Plots were placed within 10m of the forest edge, with northeast to northwest exposure. Regenerating seedlings of other species as well as aspen suckers were regularly removed from plots. Leaf litter was removed from open plots in spring 1999 to maintain similar germination conditions between exclosures and open plots.

iv) germination census

The germination period under field conditions is mid-May through early August, with 75-100% of germination complete by early July (Nienstaedt and Zasada 1990). Germination of seeds sown in June 1998 was censused in each exclosure and open plot on

8 August 1998, while that of seeds sown in September 1998 was censused on 1 July 1999. Seeds sown in spring were exposed to predation for six weeks, while seeds sown in fall were exposed for over 9 months. Searches for seedlings were extended beyond the area of the open plots, as a small number of seeds were transported outside of the plot boundaries by rainfall.

No natural white spruce seedlings would have germinated in experimental plots between the spring seed sowing in 1998 and the germination census in August, since the area had just previously been scarified (organic layer was completely removed) and no natural seed rain would have occurred before the census. Seed rain in the fall of 1998 was low. However, some recruitment due to natural seed in the experimental plots was possible. To correct for this, I quantified natural "background" levels of white spruce recruitment in the fall-sown half of each open plot at the same time as the germination census in July 1999. At each replicate, I quantified the density of naturally occurring seedlings in plots placed on mineral seedbed adjacent to the sown plots, and subtracted the average number of germinants from the number of seedlings censused in each open plot. To make the same correction for the exclosures, the number of new (natural) seedlings in the spring-sown half of each exclosure was counted, and subtracted from the number of fall-sown seedlings censused on the other half of the plot. This assumed that the same number of natural seedlings would have germinated on either side of the exclosure. "New" seedlings were distinguished from those germinating from the spring 1998 sowing by their size. New seedlings in the spring-sown half of each plot were much smaller than seedlings from sowing in spring of 1998, and therefore easily distinguished. Low viability of white spruce seed makes it unlikely that germinants in 1999 were from seed sown in spring of 1998. No natural seedlings were found outside of experimental plots with the exception of a few at two different replicates, so corrections were minimal.

The fate of seeds and seedlings in exclosures represented non-viability and natural mortality (from drought or lack of germination microsite, for example), independent of seed predators. The difference in the number of seedlings between exclosures and open plots represented the loss of recruitment to predators above and beyond these other sources of mortality.

Small mammal abundance

Live-trapping sessions were conducted in June and September 1998, to quantify the relative abundance of small mammals in the vicinity of each replicate of recruitment plots. This allowed me to test the importance of local small mammal abundance to recruitment density in the open plots. Small mammals were trapped in a 50m x 50m grid overlaying each experimental replicate (Figure 3.1), as this encompassed the territories (maximum 50m diameter for red-backed voles; Weaver 1996, R. Moses, *pers. comm.*) of animals most likely to forage in the plots. One Victor Tin Cat multiple-capture trap (ECKO Canada Inc., Niagara Falls, Ontario) was placed at each trap station. Stations were located at 25m intervals, for a total of nine traps in each grid. Three traps were located 25m into the forest, three were along the forest-cutblock interface, and three were 25m into the cutblock. Trap saturation did not occur on any trapping grid.

Traps were pre-baited for 5 days with sunflower seeds before each trapping session. Cotton bedding was provided in each trap for insulation. Sunflower seeds were replenished as necessary and an apple slice was provided for moisture. Traps were covered with woody debris and leaves. They were set for 5 consecutive nights and checked each morning, at which time individuals caught were identified to species, classified as adult vs. juvenile, and identified as new or previously caught (marked). Unmarked individuals were marked with picric acid on their abdomen, and released at the point of capture.

The number of unique individuals (adults and juveniles) was used as a measure of relative abundance of small mammals at each experimental replicate. The abundance values of mice and voles at each replicate in June were used as two covariates in the analysis of recruitment differences between spring-sown experimental plots, and abundance values from trapping in September were used as two covariates in the analysis of fall-sown plots.

Seed Removal Experiments

I used seed removal experiments to measure the direct seed consumption rate for different seed densities at the forest edge versus within the cutblock. I measured white spruce seed removal rates between May and August 1999, by counting the number of

uneaten seeds remaining in seed patches at monthly intervals. My seed patches consisted of greenhouse trays ($0.15m^2$), lined with insect screening and partially filled with locally collected soil. Seeds were scattered onto the soil surface, using the same three seed densities as for the germination trials in 1998. Before being put out in the trays, seeds were microwaved for 15 minutes on high power, to kill the embryo and prevent germination in the field. Holes in each tray allowed water to drain.

Seed trays were placed in the same three cutblocks as used in the recruitment experiment. Two replicates were placed in two cutblocks, and one replicate in a third cutblock, for a total of five replicates. Each replicate consisted of four sets of trays (for four monthly collection times), each with three seed densities at the forest edge (0m) and within the cutblock (100m from forest edge) (Figure 3.2). Trays were frequently damaged by animals, reducing the sample size of many replicates. Measuring seed removal both at and away from the forest edge allowed me to determine if foraging behaviour at the forest edge was different than within the cutblock. A distance of 100m from the forest edge was chosen to represent conditions within the cutblocks. This distance exceeds the average diameter of a small mammal territory, thereby insuring that individuals with territories in the cutblocks (rather than individuals from the forest) were foraging in those trays. This allowed me to determine if seeds dispersed close to the forest edge and those dispersed within cutblocks (from seed trees) were equally vulnerable to predation. Trays were set up in a linear fashion parallel to the forest edge, with at least one meter between trays and 50m between replicates. All replicates were placed in the field between 5 and 7 May 1999, and one set from each replicate was collected monthly from June to September 1999. I chose monthly intervals as a balance between logistical constraints and sampling frequently enough to provide information on temporal patterns of foraging.

At each collection time, I sifted out as much soil as possible from the trays using the insect screening lining each tray. The mesh size was too small for spruce seeds to go through. The remaining soil was brought to the laboratory to count the seeds. Soil samples were further sieved using nested soil sieves (2.0, 1.4 and 1.0mm) to isolate the seeds. Rodent tracks in the trays and chewed seed coats in the soil samples provided evidence of predator identity. Small mammal abundance was not measured in 1999.

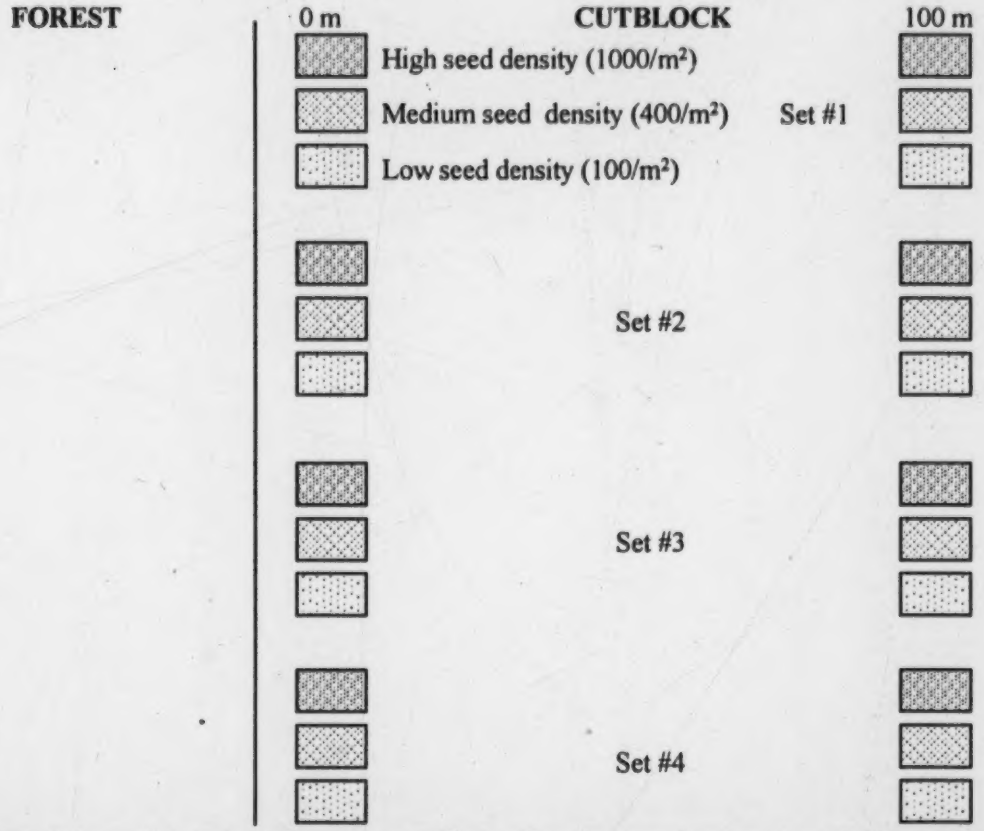


Figure 3.2: Schematic representation of one replicate of seed removal trays. A total of 5 replicates was placed in three cutblocks. Trays were a minimum of 1m apart, and replicates were separated by a minimum of 50m. One set of trays from each replicate was collected monthly between May and August 1999.

Data Analysis

i) recruitment plots

I analyzed the spring and fall recruitment data using Analysis of Covariance (ANCOVA). The dependent variable was the number of seedlings that germinated in each plot. The abundance values of mice and voles at each replicate in June were the two covariates in the analysis of spring-sown recruitment plots, and abundance values at each replicate in September were the two covariates in the analysis of fall-sown plots. The two factors tested were: predator presence/absence (2 levels, fixed factor), and seed density (3 levels, fixed factor).

Within-site variability is common in many seed predation studies (literature review in Hulme 1993), so I initially ran a model in which each pair of open and exclosure plots was treated as a separate block. Since differences between these blocks were not significant, I chose to run the model with the three cutblocks treated as blocks (random effects), in order to explore the effect of variation within versus among cutblocks. The three replicates in each cutblock were treated as random effects and nested within cutblocks, so that variation due to replicates could be partitioned from that due to cutblocks. The significance values of the main factors tested were similar in both models.

I initially ran two models (spring and fall data) with all interactions, however, only the predator by seed density interaction was significant. The analyses were then redone without the other interactions (that portion of the variation was added to the error term). The abundance values of the two small mammal species at each replicate were included as covariates in the analyses, to investigate their importance to seedling recruitment. However, they were not significant and did not affect the significance values of any factors, and were removed from the models. Therefore, the ANOVA model was: $Y_{ijkl} = \mu + P_i + D_j + C_k + R_i(C_k) + (PD)_{ij} + e_{ijkl}$, where Y is the number of seedlings recruiting in a plot, μ is the population mean, P is predator presence/absence, D is seed density, C is cutblock, R(C) is replicates within cutblocks, PD is the predator by density interaction, and e is the residual error. Variance increased as recruitment density increased, so the data were square root transformed before analysis, using $X = \sqrt{X+0.5}$ (Zar 1996). Subsequent to the ANOVA, Tukey multiple comparison tests were used to test for

differences in recruitment between the three seed densities. I used paired t-tests to test if recruitment density was significantly different between paired exclosures and open plots.

I tested for a significant difference in seedling recruitment density in open plots between the three seed densities, using a one-way ANOVA. The number of seedlings in open plots was the dependent variable. Seed density (3 levels, fixed factor) was the factor tested. The three cutblocks were treated as three blocks (random effects) in the model. The three replicates in each cutblock were nested within cutblocks.

ii) seed removal experiments

I analyzed the seed removal data using Analysis of Variance (ANOVA). The dependent variable was the number of uneaten seeds in each tray. The three factors tested included: seed density (3 levels, fixed factor), months of exposure (4 levels, fixed factor), and position relative to the forest edge (2 levels, fixed factor). The three cutblocks were treated as three blocks (random effects) in the model. The two replicates in each cutblock were treated as random effects and nested within cutblocks, so that variation due to replicates could be partitioned from that due to cutblocks. I initially ran the model with all interactions. Only the month by cutblock interaction was significant, so it was retained in the model. I also retained all other interactions including month, to show that the significant cutblock by month interaction was solely responsible for the lack of significance of the main factor month (despite a distinct trend in the data). I also included the density by position interaction in the model, as this interaction was of interest to me, and is commonly tested in foraging behaviour studies (e.g. Newman and Caraco 1987). Other interactions were removed from the model and that portion of the variation was added to the error term. The ANOVA model was: $Y_{ijklmn} = \mu + D_i + P_j + M_k + C_l + R_m(C_l) + (MC)_{kl} + (DM)_{ik} + (PM)_{jk} + (DP)_{ij} + (DPM)_{ijk} + e_{ijklmn}$, where Y is the number of uneaten seeds in a tray, μ is the population mean, D is the density of seeds, P is the position of the tray (forest edge, cutblock interior), M is the number of months of exposure, C is the cutblock, R is the replicate within a cutblock, and e is the residual error.

My sample sizes were not equal due to damage to the trays from animal activity. ANOVA is not as robust against non-normally distributed data when sample sizes are

unequal, so I log transformed the positively skewed seed count data to normalize the distribution (Zar 1996).

RESULTS

Small mammal community

A total of 156 individuals (adults and juveniles) were trapped in the study area in June, and 218 in September. *Clethrionomys gapperi* (southern red-backed vole) was the most common small mammal species trapped in the study area, followed by *Peromyscus maniculatus* (deer mouse). Red-backed voles made up 88.5% and 75.2% of the total number of animals captured in June and September, respectively. Deer mice made up 7.7% and 17.9% of the total number of animals captured in June and September, respectively. Several *Microtus pennsylvanicus* (meadow vole) individuals and one shrew (*Sorex* sp.) were also caught in the traps.

The density of voles at each replicate averaged 27.2/ha (5.3 – 55.1) and 32.4/ha (23.1 – 42.6) in June and September, respectively. The densities of red-backed voles in this study are considerably higher than the vole densities reported by Moses and Boutin (in review), who trapped over a four-year period (1993-1996) within 20 km of my study sites. They trapped in cutblocks with 10% residual canopy cover, similar to cutblocks in this study (average 11% residual). They report vole densities averaging 6.3/ha (1.3 – 11.5) and 17.2/ha (4.1 – 27.9) in spring and fall, respectively.

The density of mice trapped at each replicate in this study was considerably lower than the density of voles, averaging 2.4/ha (0 – 10.7) and 7.7/ha (0 – 17.8) in June and September, respectively. The average density of deer mice in this study was lower than that of Moses and Boutin, who reported average densities of 6.3/ha (0 – 12.3) and 16.3/ha (4.3 – 24.6) in spring and fall, respectively. Trapping data from yet another study within 3 km of my research sites indicated that small mammal abundance in spring 1998 was high (approximately 2-7 times higher) relative to the spring 1997 (J. DeGroot, *pers. comm.*), possibly due to high abundance of voles.

Density estimates from this study were likely inflated due to the small size of my trapping grid (0.25ha), compared to the trapping grid used in the study by Moses and

Boutin (6ha). As grid size gets smaller, a higher proportion of animals will have only part of their home ranges overlapping the grid, resulting in edge effects (Bondrup-Nielsen 1983). In an attempt to correct for edge effects, I added half of the inter-trap distance to each side of the grid before calculating animal density (Krebs 1989).

Impact of small mammals on seedling recruitment

i) spring seeding trial

There were no significant differences in recruitment among cutblocks (blocks), however, replicates were significantly different (Table 3.1). Investigating recruitment patterns in each replicate individually revealed that recruitment in one replicate deviated from the pattern evident in all other replicates, due to an extremely low number of seedlings in one high seed density exclosure. This may have been largely responsible for the significance of replicates in the model.

The presence of seed predators was associated with a significant reduction in seedling recruitment (Table 3.1, Figure 3.3). Although the predator by density interaction was not significant (Table 3.1), results suggest that the effect of predation varied with seed density. Seed predators reduced recruitment by 40.9%, 62.5%, and 28.7%, in high, intermediate, and low seed density plots, respectively (Figure 3.3). Recruitment in high and intermediate seed density open plots was significantly lower than in small mammal exclosures (paired t-tests, $p < 0.001$), whereas recruitment in low density open plots was not significantly lower than in exclosures (paired t-test, $p = 0.152$).

There were significant differences in recruitment among all three seed densities (Table 3.1, and Tukey tests, $p < 0.01$). Recruitment density increased with increasing seed density in open plots and small mammal exclosures (Figure 3.3). Recruitment in high seed density exclosures was 10.4 times higher than in low density exclosures. This difference was 8.4 in open plots. The difference in recruitment density in open plots between the three seed densities was significant ($F = 22.615$, $df = 2$, $p < 0.001$). This indicates that, when seeds were exposed to predation for six weeks, seed predators did not reduce recruitment down to a constant density across all seed densities (Figure 3.3).

No consistent pattern with seed density was evident in the average proportion of seeds germinating in open plots (19.8 – 28.9%; Figure 3.4). The average proportion of seeds germinating in exclosures was fairly constant across all seed densities (40.6 – 52.8%; Figure 3.4).

Table 3.1: Results of analysis of variance for spring-seeded recruitment plots, testing the effects of seed predators and seed density on the number of seedlings recruiting in experimental plots. Seed predators were present (open plots) or absent (exclosures). The seed densities tested were: 1000, 400, and 100 seeds/m^2. Three replicate sets of plots were placed within each of three different cutblocks (Blocks).

Source of variation	$df_{num.}$, $df_{denom.}$	*MS*	*F*	*p*
Predator	1, 40	79.061	19.407	<0.001
Seed Density	2, 40	286.991	70.446	<0.001
Block	2, 6	5.148	0.378	0.700
Replicate(Cutblock)	6, 40	13.601	3.339	0.009
Predator*Density	2, 40	10.858	2.665	0.082
Error	40	4.074		
Total	53			

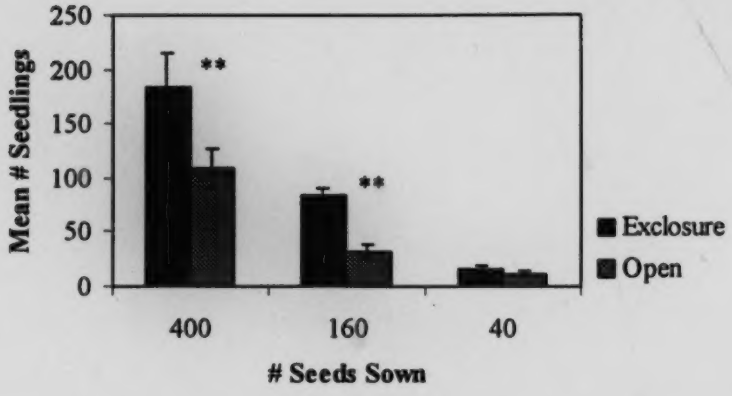


Figure 3.3: The mean number of seedlings in small mammal exclosures and open plots ($0.4m^2$), across three seed-sowing densities. Seeds were exposed to predation for six weeks between June and August. Each bar represents the mean from nine plots. Error bars are $\pm$ 1 Standard Error. The number of seedlings in exclosures was significantly higher than in open plots at high and intermediate seed densities (paired t-tests,** $p<0.01$). Recruitment was significantly different among all 3 seed densities (Tukey tests, $p < 0.01$).

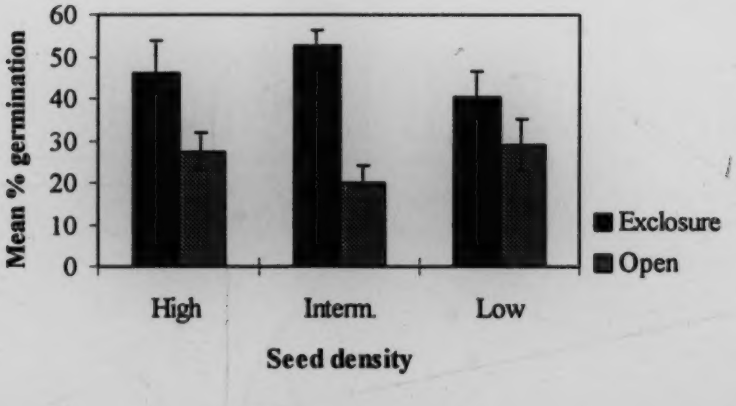


Figure 3.4: The mean proportion of seeds germinating in small mammal exclosures and open plots ($0.4m^2$), across three seed-sowing densities. Seeds were exposed to predation for six weeks between June and August. Each bar represents the mean from nine plots. Error bars are $\pm$ 1 Standard Error. No statistical tests were performed on these data.

ii) fall seeding trial

I found no significant differences in recruitment among cutblocks (blocks), or the replicates within cutblocks (Table 3.2). The presence of seed predators was associated with a significant reduction in seedling recruitment (Table 3.2, Figure 3.5). Recruitment in open plots was significantly lower than in small mammal exclosures at all three seed densities (paired t-tests, $p < 0.001$, Figure 3.5). The significant predator by seed density interaction (Table 3.2) indicated that the effect of predation on recruitment was dependent on the initial seed density. Seed predators reduced recruitment by 90.5%, 82.6%, and 65.8%, in high, intermediate, and low seed density plots, respectively (Figure 3.5).

There were significant differences in recruitment among all three seed densities (Table 3.2, and Tukey tests, $p < 0.01$). Recruitment density increased with increasing seed density in exclosure plots (Figure 3.5). Recruitment in high seed density exclosures was 8.4 times higher than in low density exclosures. However, the difference was reduced to 1.6 in open plots. In open plots, the difference in recruitment density between the three seed densities was not significant ($F = 2.85$, $df = 2$, $p = 0.088$). This indicates that when seeds were exposed to predation for nine months, seed predators reduced recruitment down to a constant density across all seed densities (Figure 3.5). The threshold seedling density was approximately 15 seedlings/m^2 (based on low density open plots, Figure 3.5). Assuming the average germination rate of 42% (black bars in Figure 3.6), a threshold of 36 seeds/m^2 were remaining after predation.

The average proportion of seeds germinating in open plots tended to increase with decreasing seed density (3.9 - 15%; Figure 3.6), so a higher proportion of seeds escaped predation when initial seed density was low. The average proportion of seeds germinating in exclosures was constant across all seed densities (40.7 – 43.9%; Figure 3.6). Therefore, there was no evidence of density dependent mortality across the seed densities tested.

Table 3.2: Results of analysis of variance for fall-seeded recruitment plots, testing the effects of seed predators and seed density on the number of seedlings recruiting in experimental plots. Seed predators were present (open plots) or absent (exclosures). The seed densities tested were: 1000, 400, and 100 seeds/m^2. Three replicate sets of plots were placed within each of three different cutblocks (Blocks).

Source of variation	$df_{num.}$, $df_{denom.}$	*MS*	*F*	*p*
Predator	1, 40	69624.423	198.54	<0.001
Seed Density	2, 40	28115.352	80.17	<0.001
Block	2, 6	1062.019	3.79	0.086
Replicate(Cutblock)	6, 40	280.204	0.80	0.576
Predator*Density	2, 40	21940.019	62.56	<0.001
Error	40	350.691		
Total	53			

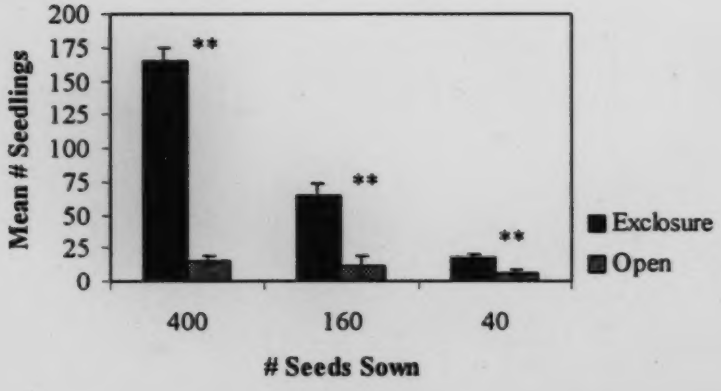


Figure 3.5: The mean number of seedlings in small mammal exclosures and open plots ($0.4m^2$), across three seed-sowing densities. Seeds were exposed to predation for nine months, between September and July. Each bar represents the mean from 9 plots. Error bars are $\pm$ 1 Standard Error. The number of seedlings in exclosures was significantly higher than in open plots at all seed densities (paired t-tests, ** $p < 0.01$). In open plots, recruitment was not significantly different between the 3 seed densities ($p = 0.088$).

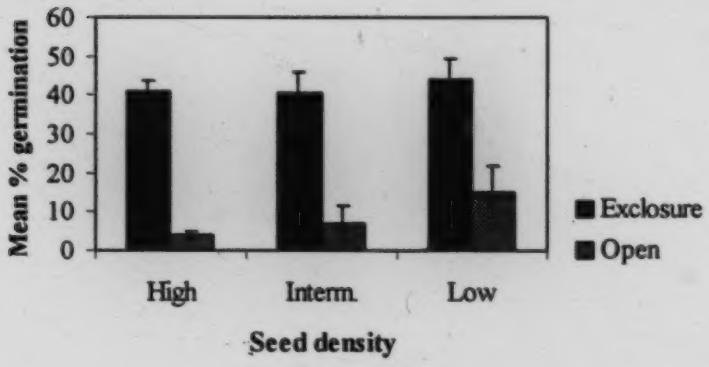


Figure 3.6: The mean proportion of seeds germinating in small mammal exclosures and open plots ($0.4m^2$), across three seed-sowing densities. Seeds were exposed to predation for over nine months, between September and July. Each bar represents the mean from 9 plots. Error bars are $\pm$ 1 standard error. No statistical tests were performed on these data.

Seed removal experiments

The density of uneaten seeds in the trays increased significantly with initial seed density (Figure 3.7, Table 3.3). Foraging behaviour was not significantly different at the forest edge versus within the cutblock ("Position"), or among cutblocks or replicates (Table 3.3). The density of uneaten seeds tended to decrease with the number of months that seeds were exposed to predators until the third month (Figure 3.7), however this was not statistically significant (Table 3.3). The effect of length of exposure on foraging was not independent of the cutblock that the trays were in, as indicated by a significant month by cutblock interaction (Table 3.3). Investigating the effect of length of exposure for each cutblock individually revealed that in two of the cutblocks the density of uneaten seeds did indeed decrease with time over all four months, however, this trend was reversed in one of the three cutblocks. Only one replicate of trays was collected in that cutblock, so the sample size to support this reverse trend is small.

After one month of exposure, the density of uneaten seeds in high seed density trays was 6.4 times higher than in low density trays (Figure 3.7). This difference tended to decrease with time, such that after four months of exposure the density of uneaten seeds in high seed density trays was only 3.5 times higher than in low density trays. However, the

density by month interaction was not statistically significant (Table 3.3). Seed predators did not reduce seed density to a similar level across the different seed densities, over the four months of exposure. At month 3, when the density of uneaten seeds was the lowest, between 8 and 38 seeds/m^2 were remaining in the seed trays (Figure 3.7). The effect of initial seed density on the density of remaining seeds was also independent of whether trays were located at the forest edge or within the cutblock (density by position interaction, Table 3.3).

The average proportion of uneaten seeds tended to increase with decreasing seed density (Figure 3.8), indicating that a higher proportion of seeds escaped predation when initial seed density was low. The overall average proportion of seeds remaining in the trays was 7.7%, ranging between 10.6 and 5.4% in low and high seed density trays, respectively.

Table 3.3: Results of analysis of variance testing the effects of seed density, tray position, and months of exposure to predation on the density of uneaten white spruce seeds remaining in trays. The seed densities tested were: 1000, 400, and 100 seeds/m^2. Foraging was compared between trays at the forest edge and 100m into the cutblock, and between trays exposed for one to four months. Trays were placed in three different cutblocks (Blocks). Model was unbalanced due to missing trays.

Source of variation	$df_{num.}$, $df_{denom.}$	*MS*	*F*	*p*
Density	2, 69	2.328	31.056	<0.001
Position	1, 69	0.0044	0.059	0.808
Month	3, 6.63	0.0282	0.140	0.933
Block	2, 4.84	0.201	0.763	0.515
Replicate(Cutblock)	2, 69	0.120	1.606	0.208
Month*Cutblock	6, 69	0.221	2.951	0.013
Density*Month	6, 69	0.0384	0.513	0.797
Position*Month	3, 69	0.0304	0.406	0.749
Density*Position	2, 69	0.0799	1.066	0.350
Density*Position*Month	6, 69	0.0891	1.189	0.322
Error	69	0.0749		
Total	102			

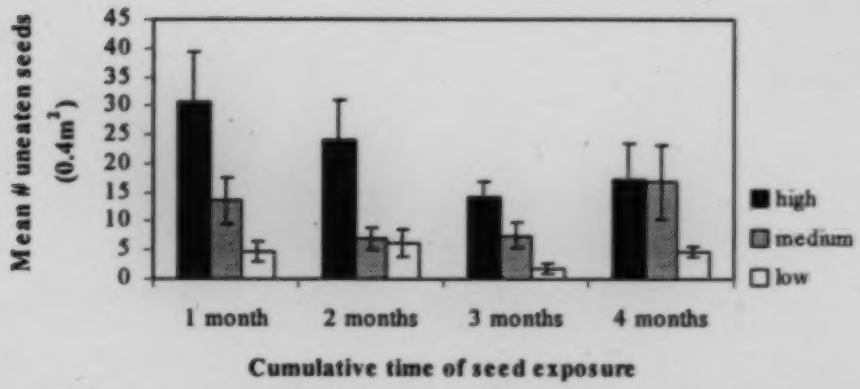


Figure 3.7: The mean density of uneaten white spruce seeds in trays exposed to predation for up to four months, between May and August 1999. Densities shown are converted to $0.4m^2$ to facilitate comparison with the number of seedlings in recruitment plots in Figures 3.3 and 3.5. The seed densities tested were: 1000 (high), 400 (medium) and 100 (low) seeds/m^2. Error bars are $\pm$ one Standard Error. Only seed density had a significant effect on the density of uneaten seeds in trays ($p < 0.001$).

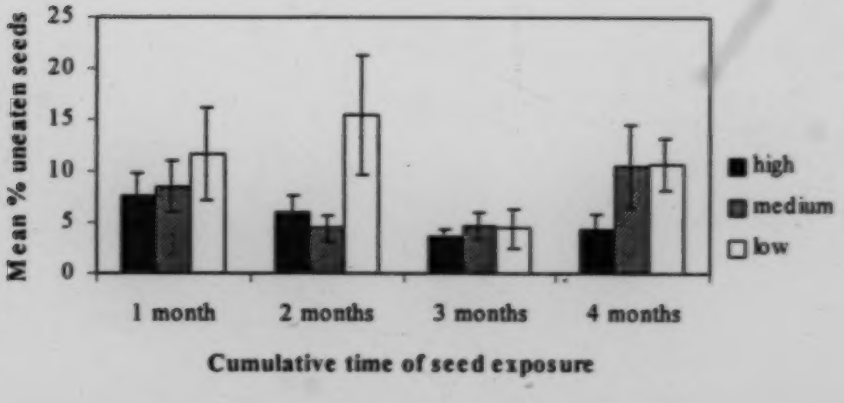


Figure 3.8: The mean percent of uneaten white spruce seeds in trays exposed to predation for up to four months, between May and August 1999. Seed densities are the same as in Figure 3.7. Error bars are $\pm$ one Standard Error. No statistical analysis was performed on these data.

DISCUSSION

Impact of seed predation on recruitment

Post-dispersal seed predation reduced recruitment density of white spruce three- to ten-fold in experimental plots exposed to predators for nine months, relative to plots with predators excluded. Therefore, post-dispersal seed predation is an important limiting factor of white spruce recruitment on mineral soil in logged areas. Some studies of other tree species have also found large impacts of post-dispersal predation on recruitment. Cornett *et al.* (1998) found that excluding post-dispersal seed predators increased recruitment two-fold for balsam fir (*Abies balsamea)* and five-fold for white pine (*Pinus strobus*) in mixed conifer-deciduous forest. Gashwiler (1967) reported that excluding small mammals and birds increased recruitment seven-fold for Douglas-fir (*Pseudotsuga menziesii*), three-fold for western hemlock (*Tsuga heterophylla*), and four-fold for western redcedar (*Tsuga heterophylla*). The studies by Radvanyi (1966, 1970) quantified the magnitude of white spruce seed loss to post-dispersal predators, but did not determine whether predation limited seedling recruitment.

Hulme (1993) reviewed 36 studies of post-dispersal seed predation by small mammals in temperate and tropical forests, grasslands, and deserts. Many of these studies found significant variation in predation rates due to habitat type, seed species, and time. Most studies on the effect of post-dispersal predation on seedling recruitment have not considered the interaction of predation with seed density. For white spruce, which exhibits large annual fluctuations in seed production, this relationship is important in order to predict recruitment patterns over time.

Seedling recruitment in plots with seeds exposed for nine months was reduced by 90% in high seed density plots, but only 66% in low density plots. This resulted in no significant increase in recruitment across a ten-fold increase in seed-sowing density. My data show that a higher proportion of white spruce seeds exposed to predators recruited under low seed density conditions. Shaw (1968) found similar results in sessile oak (*Quercus petraea*), also a masting species. The proportion of seedlings recruiting when there was a light acorn crop increased three-fold over that of a year of heavy acorn production. However, these results contradict what would be expected if mast seeding

evolved to satiate predators. Mast years are thought to be an adaptation to satiate seed predators (so that their consumption rate plateaus below the density of seeds available), increasing the probability that seeds will survive in those years (Janzen 1971). I had therefore expected that a lower proportion of seeds would be consumed in the high seed density plots, resulting in higher recruitment.

There are several possible explanations for why my data do not conform to that predicted by the predator satiation theory. The first explanation is that the experimental approach taken in this research operated on a much smaller scale than the home range size of a small mammal (average 590m^2 for *Peromyscus*, Wolff 1984). I altered seed density in small, artificial patches, set on a background of low food availability (natural seed rain in the fall of 1998 was lower than all experimental seed densities). However, in a mast year, the entire home range of an individual (within dispersal distance of seed sources) would contain a high density of seeds. Hulme and Hunt (1999) found no evidence for predator satiation of woodmice *(Apodemus sylvaticus)* with increasing seed density in experimental plots. It is unlikely that predators would be satiated by the high seed densities tested in my experimental plots, so my results represent the functional response of individuals to seed density in small patches.

Secondly, my experimental design did not test the effect of a numerical response of predator populations to seed production (seed density) (Holling 1959). Studies in Europe and the United States have found that mast seed crops allow overwinter breeding and increase overwinter survival of mice and voles, resulting in rodent outbreaks the following summer (Wolff 1996, Gashwiler 1979, Pucek *et al.* 1993, Jensen 1982). In these systems, small mammal populations are limited by low seed abundance during the intermast period. They are therefore unable to consume the entire mast crop. I manipulated seed density in my experimental plots as an attempt to mimic years of variable seed production. However, this method did not allow me to test the effect of year to year fluctuations in small mammal populations on the proportion of seeds consumed. This may have important implications for predator satiation, if mouse and vole populations respond numerically to white spruce seed production in the mixedwood forest. Therefore, comparing recruitment across seed densities provides insight into the functional response

of small mammals to white spruce seed density, rather than a test of the predator satiation hypothesis. Evidence for predator satiation in the literature is usually based on long-term field studies of seed production and survival, rather than manipulative experiments (e.g. Crawley and Long 1995).

Since small mammals reduced recruitment in experimental plots down to a constant density (approximately $15/m^2$) across all seed densities tested, it seems likely that they could reduce that spatial patchiness of white spruce recruitment in cutblocks. Rodents are known to be density-dependent foragers who do not forage randomly in a heterogenous environment where food is patchily distributed (Price and Jenkins 1986, Vickery 1978). Cutblocks with white spruce seed trees spaced randomly will have spatially variable seed rain (see Chapter 2), because most white spruce seeds are dispersed within 100m from the seed source (Dobbs 1976). Data from recruitment plots indicates that, by consuming proportionally more seeds from high density patches, seed predators may reduce the patchiness of recruitment across seed tree cutblocks. High vole densities are known to reduce spatial heterogeneity in plants with patchy distributions by virtually eliminating young tree seedlings within several months to a year (Ostfeld *et al.* 1994). If voles forage similarly on seeds, this may result in reduced patchiness of white spruce recruitment.

Several factors suggest that the results obtained in the recruitment plots may represent the maximum effect of predation on recruitment density of white spruce. First, I tested an ideal seedbed for white spruce germination. Mineral soil, whether from fire or mechanical site scarification after logging, has high germination success for white spruce seeds (Rowe 1955, Lees 1963). Under these conditions, a high proportion of seeds consumed by rodents would have otherwise germinated, increasing the loss of recruitment attributable to predation rather than other factors (e.g., lack of germination microsites) (Andersen 1989). Secondly, using artificial seed patches, set on a background matrix of low seed density, may have resulted in my plots acting as a draw for seed predators. Hulme and Hunt (1999), however, found that relative seed density in plots did not significantly influence the number of seeds predated. Since I did not observe a higher rate of seed removal in high density (vs. low density) seed trays with length of exposure, I do

not have strong evidence to support the notion that my recruitment results represent artificially high rates of predation due to the effects of drawing in predators.

Mouse population densities were below average in the year and location this study was conducted, I could therefore have expected low rates of seed predation. Higher seed mortality of douglas-fir and western hemlock was reported by Gashwiler (1967) in a year of high deer mouse density, relative to a year of low mouse density. Ostfeld *et al.* (1997) found an inverse relationship between the abundance of meadow voles (*Microtus pennsylvanicus*) and white-footed mice *(Peromyscus leucopus*). This resulted in low rates of seed predation in plots with high vole densities, because mice are more dependent on seeds in their diet than voles (Whitaker 1997). This relationship did not hold true for this study, since despite high vole (*Clethrionomys gapperi)* and low mouse (*Peromyscus maniculatus)* densities, high rates of predation occurred in experimental plots.

I cannot rule out the possibility that seed predators such as birds or insects (e.g. ants) were partially responsible for high rates of seed loss in my recruitment plots, since this was not directly quantified in my research. However, I know of no study on post-dispersal seed predation of conifer species that has identified birds or insects as primarily responsible for seed loss. In Radvanyi's (1966) study, only 3.5% of white spruce seeds were lost to invertebrates. Birds may have been responsible for up to 9% of the white spruce seeds that were unaccounted for in Radvanyi's study. Gashwiler (1970) identified birds and chipmunks as responsible for up to 24% of the loss of douglas-fir and up to 3% of western hemlock seeds. These losses are much lower than losses to mice and voles in those studies.

Many post-dispersal seed predation studies are conducted over very short time spans, relative to the duration of exposure to predators. In Hulme's (1993) review of 36 post-dispersal predation studies, over half (58%) of the studies were conducted for a duration of 10 days or less. In the current study, recruitment data from plots with seeds exposed for six weeks (shorter than natural duration of exposure) showed a different pattern of predation than that of plots with seeds exposed for the full duration of natural exposure (over nine months). The short-term recruitment experiment showed a significant gain in recruitment density with increasing seed density, despite high variability in

predation between plots. However, over the natural duration of seed exposure, predators were capable of reducing recruitment to a constant density, despite a 10-fold range in initial seed density. Different conclusions may be drawn from seed predation studies depending on the duration over which they are conducted.

It is risky to make generalizations regarding early recruitment stages, which are especially variable, based on data from one year (Clark *et al.* 1999, Whelan *et al.* 1991). For instance, DeSteven (1991) found that differing weather patterns across the two years of her study affected the role that seed predation played in the recruitment patterns she observed. If my study had been conducted in a year of drought for example, an overall lack of germination success may have outweighed any detectable effects of seed predation on recruitment. Fortunately, germination success in the year of study was high enough (47% and 42% in spring and fall-sown exclosures) to detect any treatment effect of small mammal exclosures on recruitment. Longer term studies would encompass a range of natural variability in weather conditions for germination and small mammal population densities, and thus provide a more reliable assessment of the role of seed predation on recruitment limitation.

Foraging behaviour of small mammals

The seed removal experiments provided a direct measure of seed consumption rate, and insight into how it is affected by the position of seed patches (forest edge or within the cutblock), and the length of seed exposure to predators. Seed predators removed 89 – 95% of seeds, across seed densities ranging from 100 – 1000 seeds/m^2. Similarly, Manson *et al.* (1998) found uniformly high levels of seed predation (approximately 99%) of red maple (*Acer rubrum*) by rodents in old-fields across a ten-fold range in seed density. On average, over 71.5% seed loss was recorded for plant species of temperate deciduous woodland, in the literature review by Hulme (1993).

There was no significant difference in the density of uneaten seeds detected between the forest edge and within the cutblock. The location of seeds relative to the forest edge might have affected predation in a number of ways. Myster and Pickett (1993) noted that leaf litter, found only close to the forest edge, contributed to lower predation rates at the forest edge by changing the detectability of seeds. Some studies have found

higher seed densities remaining in experimental patches located in open habitat, inferring greater risk of predation when farther from cover (Brown *et al.* 1988, Bowers *et al.* 1993). Sekgororoane and Dilworth (1995) trapped no deer mice beyond 10m and no red-backed voles beyond 5m into harvested areas in mixed coniferous forest. On the contrary, Weaver (1996) found that red-backed voles held territories throughout cutblocks with residual trees in mixedwood forest. Foraging behaviour of mice and voles in cutblocks in mixedwood forest seems to be independent of whether seeds are located at the forest edge, or within the cutblock. Thus, seeds dispersed from seed trees retained within cutblocks are equally vulnerable to predation as those near the forest edge.

The average density of uneaten seeds in trays tended to decrease with cumulative length of exposure, however this trend was not statistically significant. Different patterns were observed in the different replicates, indicating that spatial stochasticity is an important factor as well. In four of the five replicates, the density of uneaten seeds declined through to August. However, in one of the replicates, the average density of uneaten seeds declined through July, but then increased in August. This may have occurred because white spruce seeds begin dispersing in August (Nienstaedt and Zasada 1990). The increase in uneaten seed density in August may either reflect spatial stochasticity in foraging between replicates (Hulme 1993, Whelan *et al.* 1991) or the input of naturally-dispersed seeds into the trays.

The general decrease in the density of uneaten seeds with time indicates that a delay in germination of naturally-dispersed seeds by one month or more (e.g. due to drought) may result in a progressive decline in the number of seeds available for regeneration. It therefore seems adaptive for white spruce seeds to germinate as early in spring as weather permits, to decrease chances of post-dispersal predation. Seeds that germinate early in the growing season also increase their chances of overwinter survival (Coates *et al.* 1994).

The density of uneaten white spruce seeds was significantly greater in trays with higher initial seed density. This conforms to the pattern of recruitment observed across seed densities in the spring-sown recruitment plots. This is in contrast, however, to the pattern observed in the fall-sown recruitment plots, where predators reduced recruitment

down to a constant density (approximately 15 seedlings/m^2) over nine months of exposure, regardless of seed density. The recruitment data indicates that below a threshold density, white spruce seeds appear to lose their vulnerability to predators. This threshold seed density in open plots was 36 seeds/m^2, assuming the same average germination rate as in exclosures (42%). Based on the seed removal experiments, it appears to take longer than four months for predators to reduce high seed densities to that threshold. The density of white spruce seeds might have become equal across different seed densities if the trays had been exposed for a longer time period (ie. overwinter), however this was not tested.

Conclusions and management implications

Seeds of white spruce were subject to heavy predation after dispersal, irrespective of whether they were near the forest edge or within a cutblock. On mineral soil, up to 90% of recruitment was lost to post-dispersal predation under high seed density conditions, and up to 66% in low density conditions. This resulted in similar seedling densities in recruitment plots (approximately 15 seedlings/m^2) across a ten-fold difference in seed density, indicating the presence of a threshold seed density (36 seeds/m^2) below which white spruce seeds were no longer vulnerable to predation.

The results of this study seem to contradict the notion that more seed sources, or higher artificial seeding density, will result in a linear increase in seedling recruitment (Lyon and Robinson 1977). Spatially dispersing seed sources across cutblocks may reduce seed losses in higher density seed patches. These results suggest that artificial seeding densities higher than 36 seeds/m^2 may not necessarily increase recruitment, and that there is an advantage to seeding scarified seedbeds in spring rather than fall, because of reduced exposure time to predators.

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CHAPTER 4

GENERAL DISCUSSION

Cumulative impact of pre- and post-dispersal predation

This study provides empirical data on the magnitude and patterns of seed predation, and the cumulative impact of pre- and post-dispersal predation on white spruce regeneration after logging. Half of the white spruce cone crop produced in 1998 was harvested by red squirrels before seed dispersal, and 90% of seeds in experimental seed trays were eaten by post-dispersal predators. It is clear that some of the seeds lost to predators would have otherwise germinated, since recruitment in plots exposed to predators from fall 1998 to summer 1999 was reduced by up to 90% as compared to recruitment in small mammal exclosures. Therefore, seed predation is an important limiting factor of white spruce recruitment on mineral soil in logged areas.

Red squirrels harvested an average of 43% (30 – 55%) of cones from white spruce seed trees retained within cutblocks and 56% (48 – 63%) of cones from trees in the forest adjacent to the cutblocks. This reduced the number of seeds dispersed into the cutblocks by half. Foraging behaviour of squirrels in the cutblock was affected by the spatial arrangement of seed trees; those retained in large patches had higher cone loss (51%) than those retained as single trees (33%). After white spruce seeds are dispersed, they are subject to high levels of mortality due to lack of germination microsites, predation, and unsuitable environmental conditions. In experimental recruitment plots on mineral soil, an average of 58% of seeds did not germinate. Seed predation in the experimental plots further reduced seed germination (recruitment) by 29 – 90%, depending on the sown seed density and the length of time seeds were exposed to predation. No difference in foraging behaviour was found between the forest edge and within the cutblocks.

The cumulative impact of pre- and post-dispersal seed predation on recruitment in the cutblocks is outlined in Figure 4.1. Squirrels harvested an average of half of the seeds in cones produced in 1998. This directly reduced the number of seeds available for regeneration, because no seeds would be expected to germinate from harvested cones.

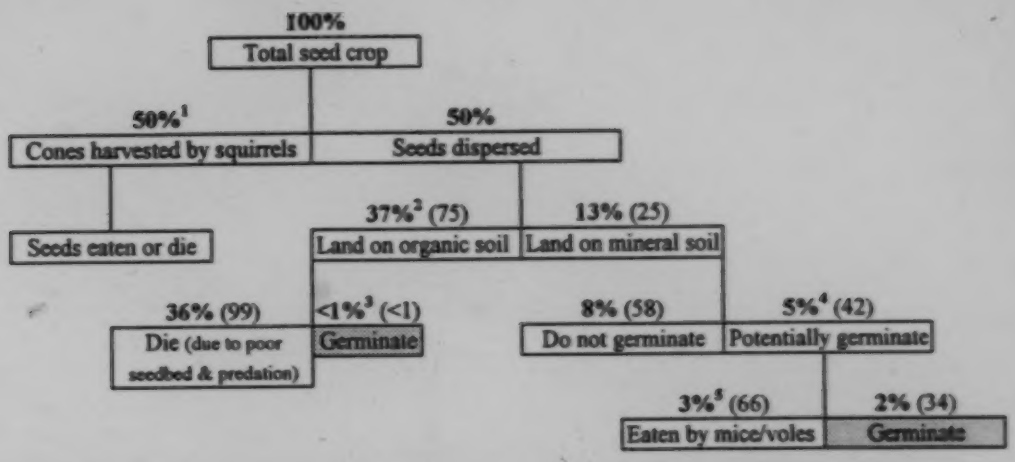

Figure 4.1: Cumulative impact of small mammals on white spruce recruitment in cutblocks with 25% mineral soil seedbed in 1998. The bold numbers above each box indicate the proportion of the total seed crop represented by that box, while the numbers in brackets indicate the proportion of the preceding level represented by that box.

[1] The overall average percent of white spruce cones harvested by squirrels from seed trees within all cutblocks and trees in adjacent forest was 50% (39 - 59%). Seeds from the remaining 50% of cones were dispersed, assuming no seeds were lost to insects or birds.

[2] This assumes that an average of 75% of the cutblock area was organic seedbed and 25% mineral, and that the proportion of seeds dispersed onto those seedbeds was the same.

[3] Nienstaedt and Zasada (1990) found that 500-1000 seeds were needed to produce 1 seedling on an organic seedbed. This includes seed mortality due to the poor seedbed, environmental conditions and predation. Therefore, less than 1% of seeds would be expected to germinate on organic soil.

[4] Average germination rate on mineral soil in exclosures was 42%. This may be an overestimate due to the high seed viability (90%) of sown seeds relative to natural seeds in a moderate seed crop year (40 - 71%).

[5] 66% of potential recruitment was lost to seed predators in low seed density open plots (100 seeds/m^2). Data from low density plots was used here because this most closely mimics the natural seed rain density from the 1998 crop. The proportion of potential recruits lost to predation could be as high as 90%, based on data from high seed density plots.

Half of the seeds produced in 1998 were not harvested by squirrels, and would have been dispersed, assuming that no seeds were lost to cone insects or birds.

An estimated 25% of the seedbed of each cutblock used in this study was exposed mineral soil (G. Grover, *pers. comm.*), therefore approximately 25% of seeds would land on mineral soil, and 75% on organic soil (Figure 4.1). Only an extremely small proportion of the seeds that were dispersed onto organic soil would be expected to germinate, as organic soil is a poor germination microsite for white spruce (Coates *et al.* 1994). I did not collect seed predation data for organic seedbeds, so I used data from literature for the germination success rate of white spruce on organic soil. Nienstaedt and Zasada (1990) report seed:seedling ratios of 500-1000:1, indicating that up to 1000 white spruce seeds may be needed to produce one seedling on organic soil in harvested areas. This ratio includes mortality due to lack of suitable germination microsites and predation, however I do not know what proportion of seed mortality on organic soil was due to predation. I assumed therefore that less than 1% of seeds landing on organic soil would germinate.

Of the seeds that were dispersed onto mineral soil, over half (58%) would have failed to germinate due to causes other than predation (non-viability, lack of microsite, unsuitable environmental conditions), representing 8% of the total seed crop (Figure 4.1). This is based on the average germination rate in exclosures on mineral seedbed. The remaining 42% of the seeds dispersed onto mineral soil (5% of the total seed crop) would have potentially germinated. It is worth noting here that the viability of the white spruce seeds sown into experimental plots (90%) was probably higher than average seed viability in moderate cone crop years (40-71%, Nienstaedt and Zasada 1990, Waldron 1965), likely inflating the proportion of potential germinants in Figure 4.1. Recruitment in low seed density (100 seeds/m^2) open plots was 66% lower than in exclosures. Thus, 66% of the potential germinants were eaten by predators, representing 3% of the total seed crop. Data from low seed density exclosures was used in Figure 4.1 because it most closely represented the density of natural seed rain in the cutblocks in 1998. Only 2-3% of the white spruce seed crop of 1998 was expected to germinate after pre-and post-dispersal predation.

Two important points emerge from Figure 4.1. First, squirrels harvested a larger proportion of the total seed crop than mice and voles did in 1998. Although we do not know the exact seed mortality rate on organic soil due to post-dispersal predation, the proportion of the total seed crop lost to mice and voles would not have exceeded the loss of seeds to squirrels. Secondly, seed mortality on organic soil in cutblocks (due to lack of suitable seedbed and predation) was likely greater than loss to post-dispersal predators on mineral soil in 1998. These points emphasize the importance of decreasing cone harvesting by squirrels, and increasing the availability of suitable seedbed in cutblocks in order to increase white spruce regeneration after logging. These points will be discussed further in the subsequent section on forest management recommendations.

I investigated the impact of squirrel cone harvests on seed rain in each cutblock by calculating the density of seed rain that would have been expected with no squirrel cone harvesting, compared to that with squirrel cone harvesting. These calculations (outlined in Appendix 4.1a and b) incorporated seed rain from seed trees and trees in the adjacent forest (control trees). The following variables were included in calculations of seed rain from seed trees in each cutblock: number of cones/tree, number of viable seeds/cone, and the number of cone-bearing seed trees/ha. The average number of cones per cone-bearing tree was calculated as described in Chapter 2 (Figure 2.2). The number of viable seeds per cone is variable, and generally increases with cone crop size (Nienstaedt and Zasada 1990). Since cone production was moderate in the year this study was conducted, I chose an intermediate value (30 viable seeds/cone) within the range reported in literature (12 – 80, Coates *et al.* 1994). In a moderate cone crop year, some white spruce trees do not produce cones. According to the cone crop rating system by Eremko *et al.* (1989), up to 50% of trees have *many* cones (in the order of thousands) in a moderate year, indicating that the total proportion of trees bearing some cones was higher. I estimated that 75% of all trees at my study sites were cone-bearing in 1998 (*pers. obs.*). These calculations provided an estimate of the seed rain from seed trees.

The following variables were included in calculations of seed rain from white spruce trees in the forest adjacent to each cutblock (Appendix 4.1a and b): the average spruce density (# stems/ha), the area (ha) of a 30m wide ring of forest around each

cutblock, number of cones/tree, and the number of viable seeds/cone. Greene and Johnson (1996) found that most seeds deposited in a clearing were contributed by trees lying within two tree heights of the forest edge. I made the conservative assumption that the area of forest contributing seeds to the cutblock was a 30m wide ring (approximately one tree height) around the cutblock. Stewart *et al.* (1998) report a mean white spruce seed dispersal distance of 15m through aspen canopy with leaves on, and 27m after leaves have fallen. It is therefore unlikely that trees beyond 30m into the forest would contribute many seeds to the cutblock.

To determine the area of a 30m wide ring of forest around each cutblock, I subtracted the area of a circle equal in size to that of the cutblock from the area of a circle with radius 30m greater. This assumed the cutblocks were circular in shape. However, since the cutblocks were more tortuous than a circle, this was an underestimate of the area of forest around each cutblock. To determine the total number of white spruce trees in the ring of mixedwood forest around the cutblocks, I multiplied the area (ha) of the ring around each cutblock by the average spruce density (# stems/ha) in the adjacent forest. I estimated that 75% of the total number of spruce trees in the forest adjacent to the cutblocks were cone-bearing. The total number of seeds dispersed was determined by multiplying the number of cone-bearing spruce trees by the number of cones/tree and the number of seeds/cone. I estimated that 30% of the seeds dispersing from trees in the forest would actually land in the cutblock. This is based on the fact that many of the seeds dispersed from trees within the forest (i.e., not right at the edge) would not land in the cutblock, and trees on the leeward side of the clearing would contribute few seeds (literature review in Coates *et al.* 1994). These calculations provided an estimate of the seed rain from the forest edge.

Table 4.1 compares the seed rain expected with no cone harvesting by red squirrels, to that with cone harvesting. The expected seed rain density was 33% (cutblock 4) to 74% (cutblock 8) lower when seed losses to squirrels were incorporated. Table 4.1 also compares the actual seed rain (assessed by seed traps) to that expected without squirrel cone harvesting (based on calculations). The density of seed rain obtained in each cutblock was extremely low and spatially variable, averaging 0 – 18.4 seeds/m^2 in different

cutblocks. This was substantially lower (average of 94%) than the estimated density of seed rain without squirrel cone harvesting. Approximately half of the difference between actual seed rain and estimated seed rain without predation was attributable to red squirrels. The remaining difference between actual seed rain and estimated seed rain without predation was possibly due to the coarse parameter estimates for calculations of seed rain density, low seed viability (e.g. low pollination success), unquantified seed losses to cone insects, birds or invertebrates, or inaccurate measurement of seed rain.

Table 4.1: Expected seed rain density (average # seeds/m^2) without and with squirrel cone harvesting from the 1998 cone crop, compared to actual seed rain density (average # seeds/m^2) from 40 seed traps in each cutblock (except cutblock 4). Estimated percent seed loss due to squirrels alone and the percent loss based on actual seed rain is presented. Expected seed rain was calculated using data from this study and from literature (see Appendix 4.1). Seed trap data were collected between August and November 1998.

	Expected Seed Rain:		Actual	% loss	% loss
Cutblock #	No predation	Squirrels	Seed Rain	(squirrels)	(actual)
1	164	76	18.4	53.7	88.8
2	53	20	3.7	62.3	93.0
3	103	56	10.4	45.6	89.9
4	111	74	N/A	33.3	N/A
5	34	12	1.8	64.7	94.7
6	97	29	2.1	70.1	97.8
7	593	153	0	74.2	100
8	113	29	9.3	74.3	91.8
Mean	**158.5**	**56.1**	**7.0**	**59.8**	**93.7**

The discrepancy between the expected seed rain density with squirrel cone-harvesting and the actual seed rain density from traps (Table 4.1) seemed to indicate that factors other than cone-harvesting by squirrels were decreasing seed rain. I did not quantify insect predation in this study; however, cone insects may destroy a substantial proportion of a cone crop (Miller 1986, Ruth *et al.* 1982). No data regarding insect infestation levels were available from Alberta Land and Forest Service or Smoky Lake Forest Nursery, as cone insect surveys are no longer done in Alberta, except in seed

orchards (D. Palamaruk, *pers. comm.*). The only information available was that white spruce cones collected in the forest management area of Alberta Pacific Forest Industries (ALPAC) generally had low levels of cone insect infestation in 1998 (Smoky Lake Forest Nursery, *pers. comm.*). Another possible explanation for the extremely low seed rain in seed traps was low pollination success due to unsuitable weather conditions during peak pollination, resulting in a low proportion of seeds with developed embryos. However, this was also not likely since rainfall in May (peak pollination period) was much lower than average (Environment Canada 1998, Appendix 4.2), favoring high pollination success (Nienstaedt and Zasada 1990).

I suspect the discrepancy between the expected seed rain density with squirrel cone-harvesting and the actual seed rain density from traps (Table 4.1) was primarily due to the method used to collect the seed rain data. Seed traps were placed in a uniform grid across each cutblock, however, seed sources were clumped and relatively few traps were placed around them. Since a large number of traps were not within the dispersal distance of most seed sources, this biased my estimate of average seed rain density. Placing traps in a grid pattern across each cutblock provided an estimate of the variability in seed rain across the cutblocks, but did not provide a good estimate of the average density of seed rain within the dispersal range of seed sources.

Seed predation by insects (e.g. ants) may have been an additional factor reducing the number of seeds in traps. Radvanyi (1966) followed the fate of radio-tagged white spruce seeds in cutblocks, and insects removed only 3.5%. My seed traps were elevated off the ground, thereby reducing the chances of seeds being depredated. Consequently, I do not suspect a large number of seeds in the traps were depredated by insects.

Management recommendations

In the past, forest managers tried to control seed losses to rodents by poison baiting (Gashwiler 1969). Not surprisingly, this met with little success, as rodents can quickly re-colonize an unpopulated area (Sullivan 1979). More ecologically-based forestry recognizes that small mammals are an integral part of our forests (Maser *et al.* 1978).

The largest measured loss of white spruce seeds in 1998 was to red squirrels (Figure 4.1). This emphasizes the importance of decreasing cone harvesting by squirrels. My results indicated that red squirrels harvest 18% fewer cones from trees retained as singles than trees in patches larger than 20 trees. Forest managers should, therefore, avoid retaining seed trees in large patches, to decrease pre-dispersal seed losses to squirrels. Furthermore, well-dispersed seed trees should reduce the spatial variability of seed rain in cutblocks. Post-dispersal predators removed more seeds from high density patches, reducing recruitment to a similar level as in low seed density patches (Chapter 3). High density patches of seeds may also be subjected to subsequent density-dependent mortality.

This study provides information to forest managers regarding the density and timing of aerial seeding in cutblocks. High seed density plots exposed to predation for nine months had a higher proportion of potential germinants lost to predators than low seed density plots. This resulted in no significant difference in recruitment density across 10-fold range in initial seed density, indicating the presence of a threshold seed density below which seeds were no longer vulnerable to predation. Based on data from these plots, this threshold density was 36 seeds/m^2. Predators did not forage plots down to this density when seeds were exposed for only six weeks (spring-sown plots). In spring-sown plots, 29 – 63% of potential germinants were lost to predation, resulting in 30 - 272 seedlings/m^2, whereas 66 – 90% were lost in fall-sown plots, resulting in 15 - 39 seedlings/m^2. The trend towards greater predation with length of exposure was also seen in the seed removal experiments. Radvanyi (1966, 1970) suggests broadcast seeding for white spruce in fall or midwinter. However, based on the predation patterns found in this study, I would recommend sowing cold-stratified seeds in spring rather than fall, to reduce exposure time to predators. I would also recommend sowing seeds at the threshold density observed in recruitment plots (36 seeds/m^2), below which predators did not forage. This seeding density should result in approximately 15 seedlings/m^2 (based on 42% germination rate in exclosures). This level of recruitment would meet regeneration standards, even after substantial seedling mortality.

In order to meet provincial regeneration standards, one white spruce seedling must be found in at least 80% of survey plots (10m^2), evenly distributed across the cutblock

(Alberta Forestry, Lands and Wildlife 1992). These surveys are done between 4 and 8 years after logging. Forestry companies relying on natural regeneration aim for initial establishment of 1 white spruce seedling/m^2, thus allowing for substantial subsequent mortality due to frost damage, light starvation, drought, leaf smothering, and herbivory (V. Lieffers, *pers. comm.*). Therefore, for successful natural regeneration using the seed tree method, sufficient cone-bearing trees should be retained to result in an average of one seedling/m^2. Recommended densities of seed trees in the literature range from 5 to 25 trees/ha (Lyon and Robinson 1977, Coates *et al.* 1994).

In Figure 4.2, I have outlined the impact of seed predation on the seed crop of one white spruce tree, with the same proportion of seeds lost at each step as in Figure 4.1. White spruce trees had an average of 1733 cones in 1998 (Chapter 2). I would have expected 948 seedlings to result from one seed tree in a cutblock with 25% mineral soil. Therefore, if 1 tree was retained per hectare, approximately 0.1 seedlings/m^2 would be expected. A density of 10 cone-bearing seed trees/ha should therefore have resulted in approximately 1 seedling/m^2.

There is no density of seed trees that will guarantee adequate regeneration, since natural variability in other important factors cannot be controlled. Based on data from the eight cutblocks used in this study, seed tree densities between 3 and 48 trees/ha did not result in sufficient regeneration to meet provincial standards in a year of moderate cone production[1]. Ten trees/ha could potentially be sufficient to regenerate cutblocks provided seed trees were well dispersed. This would result in a greater proportion of the cutblock being within the effective dispersal distance of white spruce. An added benefit of leaving seed trees as singles is that they experience less cone predation from squirrels. My recommendation of 10 seed trees/ha was also based on the assumption that no trees were lost to windthrow, and that 25% of the cutblock was mineral soil. If this was an over-estimate of the actual availability of mineral soil, seed tree densities would need to be increased to compensate for this lack of suitable seedbed. To maximize the high germination rate of freshly exposed mineral soil, seedbed scarification should be done in

[1] No natural seedlings were recorded during systematic regeneration surveys in all eight cutblocks. Data provided by Alberta Pacific Forest Industries Inc..

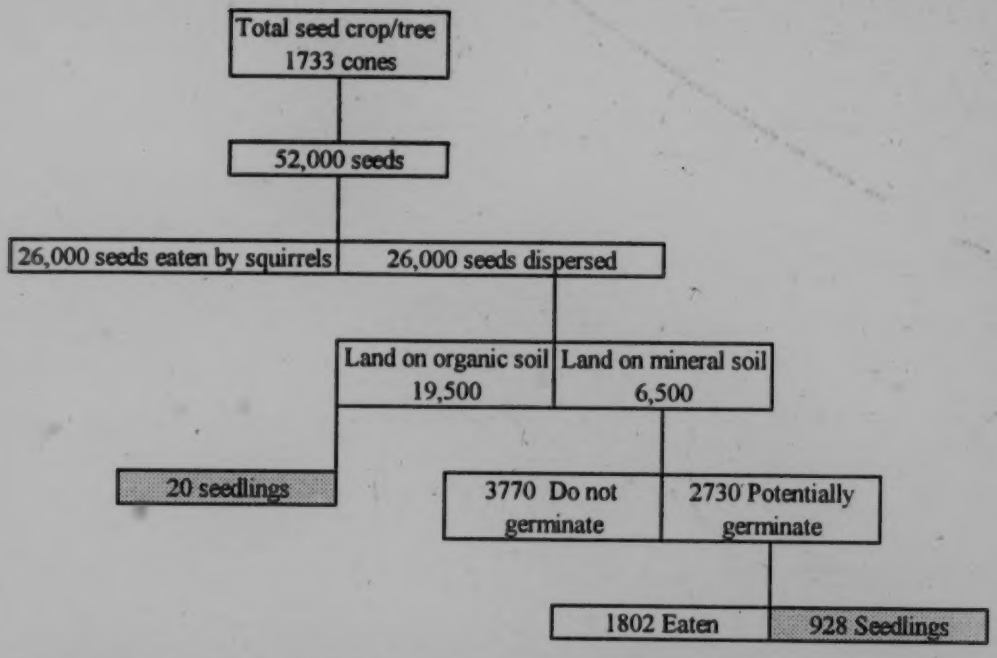

Figure 4.2: Cumulative impact of small mammals on recruitment from one white spruce tree in a cutblock with 25% mineral soil. See Figure 4.1 for the proportion of the total seed crop represented by each box, and the assumptions at each step. Data from this figure used as the basis for a recommendation of seed tree density required for natural regeneration to meet provincial regeneration standards.

the year of a large cone crop. Ideally this would occur immediately after logging, to increase the length of time seedlings have to reach the height required (50cm) to meet regeneration standards. Annual cone production should therefore be monitored so that mast years can be predicted. Cone production of the subsequent year can be predicted based on weather. Warm, dry weather during reproductive bud differentiation (July) is an indication of a potentially large cone crop, especially if the preceding crops have been poor (Eremko *et al.* 1989, Nienstaedt and Zasada 1990). Another way of predicting cone production is by counting female reproductive buds (located in the upper part of the tree crown) in fall or winter (Nienstaedt and Zasada 1990).

Figure 4.3 illustrates the estimated impact of pre-and post-dispersal predators in a mast seed year for white spruce. White spruce trees may produce up to 8000 cones in a mast year (Waldron 1965). I do not have data for the proportion of cones harvested by squirrels in a mast year. However, based on the predator satiation theory, I would expect that a lower proportion of cones would be harvested in a mast year, relative to a moderate year. Therefore, the proportion of seeds lost to squirrels in Figure 4.3 represents a maximum (50%). Based on my recruitment data (Chapter 3), post-dispersal predation compensated for higher seed densities by removing a higher proportion of potential germinants (90%). Based on these assumptions, I would expect up to 1350 seedlings to recruit from one white spruce tree in a mast year (Figure 4.3). If one seed tree/ha was retained, I would expect 0.135 seedlings/m^2, or 1.35 seedlings/m^2 if 10 trees/ha were retained. Despite higher seed production than 1998, the expected density of seedlings is not substantially higher (Figure 4.3). However, it is worth noting that the methods used to measure post-dispersal predation likely did not incorporate the effect of satiation, which would increase the proportion of seeds that escape in a mast year. Combined with the expectation that a lower proportion of cones would be harvested by squirrels, it seems likely that seedling recruitment would increase in a mast year.

Recommendations for future research

Other factors not addressed in this study, but with important implications for the spatial distribution of residual trees, are windthrow susceptibility, and habitat requirements

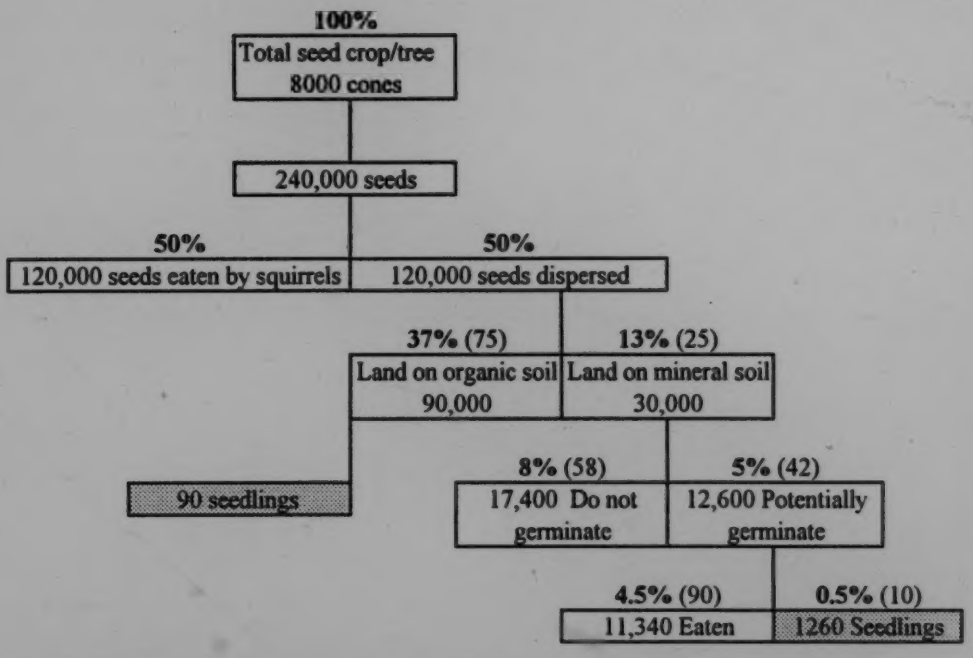

Figure 4.3: Estimated cumulative impact of small mammals on white spruce recruitment in a mast seed year in a cutblock with 25% mineral soil. The bold numbers above each box indicate the proportion of the total seed crop represented by that box, while the numbers in brackets indicate the proportion of the preceding level represented by that box. See footnotes (#1-4) in Figure 4.1 for the assumptions at each step.

of wildlife species. Isolated seed trees in cutblocks may be susceptible to windthrow (*pers. obs.*). The benefits of retaining seed trees in patches to reduce windthrow should be balanced with the increase in the proportion of cones harvested by squirrels from trees in large patches. As well, the response of other wildlife species, such as songbirds, to the density and spatial distribution of residual trees should be taken into consideration when planning cutblocks with residual trees.

One issue not addressed within the scope of this project is the long-term impacts of seed predation on the plant population. Clark *et al.* (1999) emphasize the need for longer term studies in order to assess the importance of the recruitment stage for forest regeneration. Do the effects of predation persist over time, resulting in reduced mature plant densities? Most mortality of white spruce seedlings occurs within three to five years following germination, after which time the mortality rate levels off and seedlings are considered established (Coates *et al.* 1994). During the first few years, seedlings are susceptible to high mortality levels from frost damage, smothering from leaf litter and competition with other herbaceous vegetation (e.g. *Calamagrostis*, Landhausser *et al.* 1996). Therefore, it would seem prudent to monitor experimental plots for five years to encompass the period of maximum mortality. Subsequent mortality would have to be primarily density-dependent for the loss of recruitment to predation to be over-ridden. Based on a long-term study in Ontario, mortality due to intraspecific competition in white spruce was only important much later in stand development (37 years) and at densities of 2900 stems/ha (Coates *et al.* 1994).

A second important issue not addressed by this study was the year to year fluctuations in small mammal populations. To test the predator satiation hypothesis (Janzen 1971) and incorporate a numerical response of predator populations to seed abundance, I would need to monitor red squirrel cone harvests and seed rain density throughout the range of cone crop sizes. If this was done for a minimum of 5 years, I could capture one cycle of cone production (1 mast year), since mast years occur every 2-6 years (Nienstaedt and Zasada 1990). To provide information regarding the possible role of fluctuating mouse and vole populations on seed losses, I would recommend manipulating rodent populations across experimental replicates (see Ostfeld *et al.* 1997) to

cover the range of possible densities, or repeating the experimental protocol over a minimum of five years.

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Appendix 4.1a: Calculations of expected seed rain density *without cone predation* in each cutblock

Seed rain from seed trees:	**Cutblock**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
average # cones/tree[1]	1359	2103	1549	956	2162	1417	1733	1680
x								
# seeds/cone[2]	30	30	30	30	30	30	30	30
x								
# cone-bearing seed trees/ha[3]	36	7	10	28	2	7	7	19
Expected seed rain / ha =	1,467,720	441,630	464,700	803,040	129,720	297,570	363,930	957,600
Expected seed rain / m^2 =	**147**	**44**	**47**	**80**	**13**	**30**	**36**	**96**
	+	+	+	+	+	+	+	+
Seed rain from forest edge:								
average spruce density (#/ha)[4]	44.2	22.2	181.9	125	86.8	187	1230.4	77.6
x								
area (ha) of 30m ring around cutbl.[5]	3.58	5.44	3.84	3.72	6.62	5.12	3.86	5.96
total # of spruce trees =	158.2	120.8	698.5	465	574.6	957.4	4749.3	462.5
# cone-bearing trees[3] =	118.7	90.6	523.9	348.8	431	718.1	3562	346.9
x								
average # cones/tree	1563	2639	1326	1037	1889	2187	1969	1579
x								
# seeds/cone	30	30	30	30	30	30	30	30
Total # seeds dispersed =	5,565,843	7,172,802	20,840,742	10,851,168	24,424,770	47,114,541	210,407,340	16,432,653
x								
Proportion of seeds landing in cutbl.[6]	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
÷								
size of cutblock (ha)	9.62	23.54	11.16	10.43	35.47	21.18	11.33	28.53
Expected seed rain / ha =	173,571	91,412	560,235	312,114	206,581	667,345	5,571,245	172,793
Expected seed rain / m^2 =	**17**	**9**	**56**	**31**	**21**	**67**	**557**	**17**
Total expected seed rain / m^2:	**164**	**53**	**103**	**111**	**34**	**97**	**593**	**113**

[1] Based on regression of estimated number of cones on photographs (before cone harvesting) on the actual number of cones

[2] From literature review in Coates *et al*. (1994)

[3] Not all trees are cone-bearing in a moderate cone crop year. Values presented here are 75% of total # of spruce trees.

[4] Calculated: Spruce density in adjacent forest = (% spruce canopy cover in forest x pre-harvest spruce density) / pre-harvest spruce canopy cover. See Table 2.2 for pre-harvest canopy cover values. Pre-harvest spruce density calculated as: (volume of spruce harvested + volume retained) / average volume of 1 tree = # trees harvested; # trees harvested / cutblock size = # stems/ha.

[5] Assuming most seed rain into cutblock originates from trees within 30m from edge (Greene and Johnson 1996)

[6] Assumes that only 30% of seeds land in the cutblock because not all trees right at forest edge.

Appendix 4.1b: Calculations of expected seed rain density *with squirrel cone harvesting* in each cutblock

Seed rain from seed trees:	Cutblock 1	2	3	4	5	6	7	8
average # cones/tree[1]	648	819	1058	711	988	639	649	419
x								
# seeds/cone[2]	30	30	30	30	30	30	30	30
x								
# cone-bearing trees/ha[3]	36	7	10	28	2	7	7	19
Expected seed rain / ha	699,840	171,990	317,400	597,240	59,280	134,190	136,290	238,830
Expected seed rain / m^2	**70**	**17**	**32**	**60**	**6**	**13**	**14**	**24**
	+	+	+	+	+	+	+	+
Seed rain from forest edge:								
average spruce density (#/ha)[4]	44.2	22.2	181.9	125	86.8	187	1230.4	77.6
x								
area (ha) of 30m ring around cutbl.[5]	3.58	5.44	3.84	3.72	6.62	5.12	3.86	5.96
total # spruce trees =	158.2	120.8	698.5	465	574.6	957.4	4749.3	462.5
cone-bearing spruce trees[3] =	118.7	90.6	523.9	348.8	431	718.1	3562	346.9
x								
average # cones/tree	503	897	562	478	570	525	490	414
x								
# seeds/cone	30	30	30	30	30	30	30	30
Total # seeds dispersed =	1,791,183	2,438,046	8,832,954	5,001,792	7,370,100	11,310,075	52,361,400	4,308,498
x								
Proportion of seeds landing in cutbl.[6]	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
÷								
size of cutblock	9.62	23.54	11.16	10.43	35.47	21.18	11.33	28.53
Expected seed rain / ha	55,858	31,071	237,445	143,867	62,335	160,199	1,386,445	45,305
Expected seed rain / m^2	**6**	**3**	**24**	**14**	**6**	**16**	**139**	**5**
Total Expected seed rain / m^2	**76**	**20**	**56**	**74**	**12**	**29**	**153**	**29**

[1] Based on regression of estimated number of cones on photographs (after cone harvesting) on the actual number of cones

[2] From literature review in Coates *et al*. (1994)

[3] Not all trees are cone-bearing in a moderate cone crop year. Values presented here are 75% of total # of spruce trees

[4] Calculated: Spruce density in adjacent forest = (% spruce canopy cover in forest x pre-harvest spruce density) / pre-harvest spruce canopy cover. See Table 2.2 for pre-harvest canopy cover values. Pre-harvest spruce density calculated as: (volume of spruce harvested + volume retained) / average volume of 1 tree = # trees harvested; # trees harvested / cutblock size = # stems/ha.

[5] Assuming most seed rain into cutblock originates from trees within 30m from edge (Greene and Johnson 1996)

[6] Assumes that only 30% of seeds land in the cutblock because not all trees right at forest edge.

Appendix 4.2: Monthly mean precipitation (mm) averaged from 1970 to 1997 and for 1998 alone, for Lac la Biche, Alberta*. The study was conducted in 1998.

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1970-1997	20.5	16.3	18.3	22.4	41.2	83.4	89.8	68.7	45.4	24	20.1	22.4	472.7
1998	17.7	3.9	6.4	17.3	19.6	91.4	78.6	18.8	24.2	26.5	12.6	17.7	334.5

* Lac la Biche, Alberta, is located approximately 50 km south of the study area

Source: Environment Canada